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Patterns and Rates of Nitrogen Release by Benthic Chironomidae and Oligochaeta[1]

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Metabolic mineralization of ammonium by tubificid worms and chironomid larvae appears to be an important mechanism contributing to nitrogen regeneration from aerobic lake sediments. Mean weight [ash free dry weight (AFDW)] – specific ammonium release rates ranged from 3 to 15 nmol NH_4 (mg AFDW)$^{-1} \cdot h^{-1}$ for chironomid and tubificid species collected at different times and temperatures from nearshore Lake Michigan sediments. Although mean rates of nitrogen release were similar for the two groups of benthic invertebrates, the patterns of release were different. Tubificids released nitrogen (ammonium plus primary amines) continuously, whereas chironomids released it in spurts several times per hour. Mean ammonium-release rates were generally constant with time after the animals were removed from food for both species. This implies that ammonium regeneration for these benthic animals is primarily an endogenous process. Conversely, primary amine nitrogen release often decreased with time after food removal and may reflect either egestion of partially digested materials from the animals' guts or a decrease in the metabolic pool size of free amino acids. Based on previous measurements of phosphorus release, mean molar NH_4:PO_4 ratios in excreted materials were calculated to be 15:1 for chironomids and 35:1 for tubificids.

Key words: nitrogen release, benthic invertebrates, chironomids, tubificids, ammonium excretion, amino acid release

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La minéralisation métabolique de l'ammoniac par les vers tubificides et les larves de chironomides semble être un important mécanisme de régénération de l'azote des sédiments lacustres aérobies. Le poids moyen [poids sec sans les cendres, (AFDW)] – les taux de mise en liberté de l'ammoniac varient de 3 à 15 nmol NH_4 (mg AFDW)$^{-1} \cdot h^{-1}$ chez les chironomides et les tubificides prélevés près de la côte, à des époques et des températures différentes,

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dans le lac Michigan. Bien que les taux moyens de mise en liberté de l'azote soient identiques chez les deux groupes d'invertébrés benthiques, les modalités de dégagement diffèrent. Les tubificides libèrent de l'azote (ammoniac plus amines primaires) de façon continue, tandis que les chironomides le font sporadiquement, en plusieurs jets par heure. Une fois les individus des deux groupes privés de nourriture, ils libèrent de l'ammoniac à des taux généralement uniformes dans le temps. Ceci donne à penser que la régénération de l'ammoniac chez ces organismes est avant tout un processus endogène. Inversement, la mise en liberté de l'azote des amines primaires diminue souvent avec le temps, une fois la nourriture enlevée. Ceci peut résulter soit de l'évacuation de matériaux partiellement digérés du tractus digestif, soit d'une diminution de volume du pool métabolique d'acides aminés libres. A partir de mesures antérieures de mise en liberté du phosphore, nous avons calculé que les rapports moyens NH_4:PO_4 molaires dans les matériaux évacués sont de 15:1 pour les chironomides et de 35:1 pour les tubificides.

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RECENT studies (Gallepp et al. 1978; Graneli 1979; Gallepp 1979; Holdren and Armstrong 1980) have demonstrated that the activities of benthic macroinvertebrates increase the amount of nutrient release from aerobic lake sediments into the overlying water. This increased release is a result of either bioturbation (mechanical mixing; e.g. Fisher et al. 1980) and/or metabolic mineralization of sediment organic matter. To determine the importance of the latter process to total nutrient regeneration from sediments, the amounts of nutrients excreted by component invertebrate groups should be quantified and related to the group's biomass in the sediments. Weight-specific phosphorus release rates have been measured for chironomid larvae and tubificid worms (Gardner et al. 1981). These two groups are the most abundant macroinvertebrates occurring in the nearshore regions of many lakes. If the weight-specific release rates of these groups are assumed to be typical of those for other invertebrate groups living in the sediments, macroinvertebrate excretion can account for virtually all of the phosphorus released into overlying waters from nearshore Lake Michigan sediments (Gardner et al. 1981).

In the present paper, we examine ammonium (and amino acid) nitrogen release by chironomids and tubificids (over time after feeding) to help assess the importance of these invertebrate groups to nitrogen regeneration in lake sediments and to provide insight about the metabolic mechanisms of nitrogen mineralization by these animals. Quantitative estimates of ammonium release are compared to previous measurements of phosphorus release to provide an estimate of the NH_4:PO_4 ratios in materials excreted by the two groups of invertebrates.

Methods

Tubificids and chironomids were obtained from southeastern Lake Michigan in an area near the mouth of the Grand River. They were collected with a Ponar grab from water depths of up to 11 m at irregular intervals during the periods August–October 1981 and May–August 1982. Animals retained on a 0.6-mm screen were held in native sediments within about 2°C of in situ temperatures until experiments were initiated. The interval between collection of animals and initiation of experiments varied from 1 h to 2 wk. The range of experimental temperatures was from 10 to 22°C. A single animal was used for each measurement. Chironomids were identified as *Chironomus fluviatilis* — gr. and the tubificids were mostly immatures of the type without hair setae, probably *Limnodrilus*. Ash-free dry weights (AFDW) were determined by drying each animal at 70°C for 24 h in an aluminum planchett and then ashing it at 550°C for 1 h. AFDW ranged from 0.2 to 1.0 mg for tubificids and from 0.1 to 1.5 mg for chironomids.

CONTINUOUS FLOW KINETIC STUDIES

Patterns of nitrogen excretion were examined by monitoring *o*-phthalaldehyde (OPA) reactive nitrogen (PRN, ammonium plus primary amines) in low-nutrient culture water flowing at a constant rate past the animals contained in an incubation flow cell (method A, Gardner and Scavia 1981). In most of these kinetic studies, we used a flow cell containing wet sand (Mallinckrodt, catalog No.7062; median grain size = 0.32-mm diameter). The sand reduced hydraulic dead volume in the cell and provided the benthic animals with a particle substrate. Low-nutrient culture water (20 mg $CaCl_2 \cdot 2H_2O$, 10 mg $MgSO_4$, and 20 mg $NaHCO_3$ per litre distilled water; Lehman 1980) was pumped either through the flow cell or through a bypass tube, via an Altex sampling valve, at a rate of 0.1 mL·min^{-1} with a Beckman 100-A pump. The effluent was continuously mixed with OPA reagent delivered at the same rate with a Technicon or Gilson proportioning pump.

For each measurement, about 0.05 mL sand was placed into a 0.5-mL plastic syringe barrel containing a frit (removed from a Waters Sep Pac column and cut to size). A larger flow cell containing 0.2 mL sand in a 3-mL syringe was used for some measurements to accommodate larger animals. The flow cell was assembled and the sand rinsed with culture water until PRN released from the sand was reduced to near the background levels (within ~2 mm of baseline on the recorder). A rinse time of more than 30 min was generally required to flush the sand adequately. After the animal was added to the culture water–sand mixture in the opened syringe barrel, the plunger (containing the culture water inlet

tube) was gently inserted and adjusted to form a flow cell volume of ~0.05 mL (0.2–0.4 mL for the 3-mL syringe). The syringe was tilted or inverted before final adjustment to allow sand to surround the animal in the flow cell. The flow cell was connected to the analytical system and the valve was switched to direct the culture water through the flow cell. During incubations, the flow cell was placed in an insulated water bath (Thermos bottle) to maintain desired experimental temperatures. After external PRN (transferred with the animal into the cell) was removed in an initial peak, the recorder signal (above baseline) represented PRN released from the animal as the culture water passed through the flow cell. At intervals, the sampling valve was switched to direct the culture water through a bypass loop instead of the incubation cell. This allowed examination of the baseline and of prepared solutions of ammonium (Gardner and Scavia 1981).

Quantitative Release Rate Measurements

To quantify nitrogen release, ammonium in incubation waters was fractionated from amino acids by cation-exchange chromatography and components were measured after reaction with OPA (Gardner 1978). Ammonium levels were quantified (after blank corrections) by comparing sample peak heights with those from standard ammonium solutions. Primary amine nitrogen was estimated, from relative peak areas, by assuming a primary amine:ammonium area response ratio of 7:1. This ratio was obtained by comparing fluorescent response from a standard amino acid mixture to that from a standard ammonium solution. Our primary amine measurements provided minimal estimates of free amino acid concentrations because only compounds that formed fluorescent derivatives with OPA and that eluted before ammonium on the cation-exchange column were measured. Measurements were made at discrete intervals after the animals were removed from their food source (by placement in flow cells or vials) to establish possible relationships between excretion rates and the absence of a food supply and to differentiate between "unassimilated" and "endogenous" nitrogen release. Differentiation between these two processes was based on the assumption that "endogenous" release should be relatively independent of recent food supply or gut contents, whereas "unassimilated" release should depend on the quantity and composition of food in the gut and therefore decrease with time after food removal.

Two incubation approaches were used to assess ammonium release rates. For the first, individual animals were placed in glass scintillation vials containing culture water for long (19–22 h) static incubations, and cumulative buildup of nitrogen in the water was measured at selected intervals (Gardner and Miller 1981). Individual animals were removed from their native sediments (on the day after sample collection), rinsed briefly in 200 mL of temperature-equilibrated culture water, transferred into a clean scintillation vial containing 12 mL culture water, and incubated at in situ temperature. Within 10 min after each animal was transferred to the vial, the water was gently mixed and a 1-mL sample was removed for initial ammonium analysis. Incubation waters were analyzed again at measured times of about 2, 4 (or 6), and 19 (or 22) h. Results from these incubations gave an integrated estimate of ammonium release (for intervals of 1–16 h) during the 19- to 22-h period after the animals were removed from their natural sediment environment.

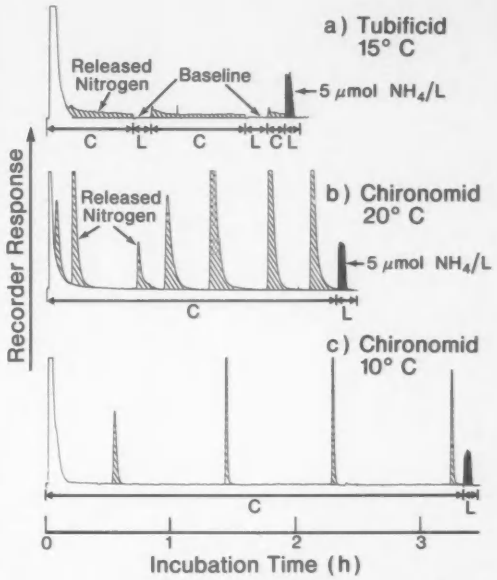

FIG. 1. Representative release rate patterns of *o*-phthalaldehyde reactive nitrogen (ammonium plus primary amines) for two groups of benthic invertebrates sampled from Lake Michigan. C and L represent flow of culture water through the incubation flow cell and bypass loop, respectively. The peak-spreading for chironomid (b) was typical and was likely caused by hydraulic mixing of materials in the flow cell. Peaks for chironomid (c) were more discrete, indicating that the animal was positioned for efficient removal of released products from the cell.

For the second approach, measurements of ammonium and amino acids accumulated in an incubation flow cell, during each of six successive 10-min intervals, provided quantitative release estimates of nitrogen release during the 1st hour after removal of the animal from food. An animal was added to the incubation flow cell (0.05 mL) and the cell was initially flushed with culture water (1.1 mL·min^{-1} for 1.5 min) to remove PRN added to the cell with the animal. At 10-min intervals thereafter, the water in the flow cell was automatically displaced with fresh culture water and transferred to the injection loop of an analyzer for ammonium and primary amine (amino acid) analysis (Gardner and Scavia 1981).

Sand substrates were not used in either approach because of potential interference due to PRN leaching from the sand during the static incubation periods. Possible non-PRN nitrogen end products (urea or uric acid) were not measured in this study, but aquatic invertebrates are generally ammonotelic (Campbell 1973). To prevent bias in comparing rates of the two groups, chironomids and tubificids were removed from the same sediment sample and examined by the same technique on a given day.

TABLE 1. Hourly frequency of PRN spurts (events per hour) for individual chironomids. After removal from food, animals were incubated in sand 18–20 h, followed by incubation without sand for 3–4 h. Mean spurt frequency for each hour given in right column. Mean hourly spurt frequency for each animal with and without sand is given at bottom of each column. Temperatures ranged from 18 to 24°C during the incubations.

			Chironomid no.				
			1	2	3	4	
	Incubation interval (h)		AFDW (mg)				
			0.33	0.51	0.73	0.99	$\bar{x}$
			Spurt frequency (events·h^{-1})				
Incubation in sand	0–1		9	6	13	8	9.0
	1–2		10	10	8	2	7.5
	2–3		14	14	4	7	9.8
	3–4		10	17	5	3	8.8
	4–5		6	12	3	3	6.0
	5–6		6	14	5	3	7.0
	6–7		4	9	5	3	5.2
	7–8		6	14	4	2	6.5
	8–9		4	16	6	2	7.0
	9–10		6	15	4	1	6.5
	10–11		3	18	6	3	7.5
	11–12		3	17	4	5	7.2
	12–13		3	18	5	4	7.5
	13–14		3	17	4	5	7.2
	14–15		3	16	8	2	7.2
	15–16		6	21	3	2	8.0
	16–17		2	10	3	1	4.0
	17–18		2	16	3	2	5.8
	18–19		11	8		1	6.7
	19–20		5	12		2	6.3
		$\bar{x}$, SE	5.8, 0.8	14.0, 0.9	5.2, 0.6	3.0, 0.4	
Incubation without sand	0–1			16	5	3	8.0
	1–2			12	8	3	7.7
	2–3			12	8	2	7.3
	3–4				4		
		$\bar{x}$, SE		13.3, 1.3	6.2, 1.0	2.7, 0.3	

Results and Discussion

PATTERNS OF NITROGEN RELEASE

Tubificids released PRN in a continuous pattern (Fig. 1a) similar to that previously observed for the pelagic cladoceran *Daphnia magna* (Gardner and Scavia 1981). Some animals occasionally released additional spurts of PRN, presumably as fecal release products; however, these generally were not quantitatively important. In contrast, chironomid larvae released PRN in discrete spurts (Fig. 1b and c). PRN was generally not observed between these spurts. The geometry of the flow cell typically caused some peak spreading and "tailing" in our record of PRN response (Fig. 1b). Peak spreading was often more pronounced for measurements done in the absence of sand because of increased mixing caused by the dead volume in the flow cell. However, actual release likely occurred almost instantaneously; when experimental animals were physically positioned by chance for efficient PRN removal from the incubation cell, narrow peaks with minimal tailing were observed (e.g. Fig. 1c). The mean spurt frequency for 10 chironomids incubated for different lengths of time at 20°C was 4.9 (SE = 1.0) spurts per hour. We did not obtain sufficient data at other temperatures to quantify the effect of temperature on spurt frequency, but three animals incubated at 15°C averaged 4.2 (SE = 2.0) spurts per hour and a single animal incubated at 10°C released PRN 1.2 times per hour on average (Fig. 1c). Three individuals removed from food for ~24 h before incubation at 20°C averaged 2.5 (SE = 1) spurts per hour.

Spurt frequency (number of events per hour), as a function of time after the animals were removed from food, was determined for four animals incubated individually over extended periods of 18–20 h. On average the spurt frequency appeared to decrease slightly with time after food removal, but patterns were not uniform (Table 1). Variations among different individuals were usually greater than changes over time for the same animal. The effect of the presence or absence of a substrate on spurt frequency was determined for three of the above animals by placing each in a sand-free cell, after the initial incubation, and observing its spurt frequency for 3–4 more hours. The presence or absence of sand did not

TABLE 2. Mean ammonium release rates and SE for chironomid larvae and tubificid worms incubated individually in 10–12 mL culture water for 19–20 h after animals were removed from their natural substrates. Animals (10°C) were collected June 1, 1982; animals (20°C) were collected on July 26 and August 1, 1982.

Organism	Approximate interval after substrate removal (h)	Mean release rate [nmol NH_4 (mg AFDW)$^{-1}$·h^{-1}]		
		$\bar{x}$	SE	(*N*)
Chironomids, 10°C	0–2	5.4	1.3	(6)
Mean AFDW=0.28 (SE=0.04) mg	2–4	4.2	1.2	(6)
	4–20	5.4	1.9	(6)
Chironomids, 22°C	0–2	14.7	3.0	(11)
Mean AFDW=0.57 (SE=0.05) mg	2–4	14.4	2.2	(11)
	4–20	11.6	1.1	(10)
Tubificids, 10°C	0–2	3.0	0.3	(5)
Mean AFDW=0.38 (SE=0.03) mg	2–4	4.1	1.1	(5)
	4–20	2.9	0.8	(5)
Tubificids, 22°C	0–2	10.8	1.5	(12)
Mean AFDW=0.58 (SE=0.06) mg	2–4	9.8	1.9	(12)
	4–20	8.4	1.5	(10)

appear to affect the spurt frequencies of these respective animals (Table 1). Frequency of PRN spurt events seemed to depend more on an animal's individual metabolism, than on the length of food deprivation or the presence or absence of a particle substrate.

To our knowledge, this is the first demonstration of exclusively pulsed release of nutrients by small aquatic invertebrates. Discontinuous release of phosphorus has been reported for ciliated protozoans (Taylor and Lean 1981) and cladocerans (Scavia and McFarland 1982), but in both cases this release (presumably resulting from defecation and/or ecdysis) was superimposed on continuous phosphorus release (presumably from excretion). The absence of mineralized nitrogen release between spurts for chironomids indicates a mechanism for storing excreted materials. Release from these animals must be regulated either through gut control or some "bladder" type mechanism. Indeed, both larvae and adult chironomids possess Malpighian tubules that may carry excretory products to the gut after metabolic conversions (Credland 1980). Alternatively, ammonium may be released directly into their guts without passing through Malpighian tubules (Chapman 1969). In either case, PRN is likely released from these animals via their guts; our data indicate that this release occurs as occasional discrete events, probably with defecation. In comparison, oligochaetes apparently excrete externally via nephridia located in individual worm segments (Brinkhurst and Jamieson 1971). Excretion products of tubificids are therefore likely released apart from the gut and, as indicated by our data, in a continuous pattern.

The different pattern of nitrogen release for chironomids, as compared with those for tubificids and other aquatic invertebrates (e.g. cladocerans; Gardner and Scavia 1981), may be linked to their developing a terrestrial adult stage. To conserve water, external surfaces of terrestrial insects are usually impermeable to water and other molecules, including ammonium (Bursell 1970). If the integument of chironomid larvae are likewise impermeable to exchange of ammonium, another mechanism for storing nitrogenous wastes for occasional release would be reasonable. Examination of a few individuals of other insect groups indicated that mayfly larvae also release PRN in spurts, whereas caddisfly larvae release it continuously. Blackfly larvae yielded spurts superimposed on a continuous PRN release pattern.

NITROGEN RELEASE RATES

Tables 2 and 3 summarize nitrogen excretion rates of tubificids and chironomids as measured by both the static and flow cell techniques. Differences in release rates between the two taxa were not significant ($P < 0.05$, Mann–Whitney test) under any given experimental condition. This contrasts to previous work on phosphorus release which showed that release rates were higher for chironomids than for tubificids (Gardner et al. 1981).

Both experimental approaches indicated that ammonium release rates were not strongly time dependent for either taxa. That is, removing animals from their food sources generally had little effect on subsequent excretion rates. These results contrast with the significant decreases in ammonium excretion rates observed over short periods (1 h) after food removal for cladocerans (Gardner and Scavia 1981; Scavia and Gardner 1982) and over longer periods (4 h) for the marine copepod *Eucalenus pileatus* (Gardner and Paffenhöfer 1982). These differences may simply reflect biological variability among the different invertebrate groups, but may also be caused by variability in the quality of ingested food. Whereas pelagic organisms often have easily mineralized, nutrient-rich food supplies (e.g. phytoplankton), benthic animals ingest the more refractory (i.e. less digestible) detrital materials (with associated microbes) in the sediments. If the benthic animals were exposed to high levels of high-nutrient, easily digested food, their release rate patterns may be closer to those of

TABLE 3. Mean release rates and SE of ammonium and amino acids by chironomid larvae and tubificid worms for six successive 10-min intervals after the animals were removed from their natural substrate and placed in an incubation flow cell (0.05 mL). Animals (12°C) were sampled June 15, 1982; animals (22°C) were sampled July 26–28, 1982.

Organism	Interval after substrate removal (min)	Mean release rate [ng at N (mg AFDW)$^{-1}$·h^{-1}] Ammonium $\bar{x}$	Ammonium SE	Amino acid $\bar{x}$	Amino acid SE
Chironomids, 12°C	0–10	4.0	0.8	1.3	0.6
N=7; Mean AFDW=0.54 (SE=0.12) mg	10–20	4.4	0.5	1.8	0.8
	20–30	4.3	0.6	0.9	0.5
	30–40	4.6	0.8	0.3	0.1
	40–50	4.3	0.7	0.5	0.3
	50–60	5.8	1.1	0.04	0.02
	$\bar{x}$ (0–60)	4.5		0.81	
Chironomids, 22°C	0–10	10.6	2.6	1.7	0.5
N=9; Mean AFDW=0.50 (SE=0.07) mg	10–20	8.4	2.2	0.4	0.2
	20–30	6.7	1.6	0.4	0.3
	30–40	6.6	1.9	0.07	0.04
	40–50	5.8	1.6	0.3	0.3
	50–60	8.5	3.8	0.1	
	$\bar{x}$ (0–60)	7.8		0.50	
Tubificids, 12°C[a]	0–10	12.1	4.7	6.0	2.1
N=7; Mean AFDW=0.47 (SE=0.09) mg	10–20	10.9	4.5	4.5	1.7
	20–30	9.0	3.1	3.2	1.5
	30–40	8.3	3.0	2.8	1.2
	40–50	7.6	2.5	2.4	0.9
	50–60	7.3	2.0	1.3	0.8
	$\bar{x}$ (0–60)	9.2		3.36	
Tubificids, 22°C	0–10	5.3	1.1	1.9	0.8
N=9; Mean AFDW=0.59 (SE=0.06) mg	10–20	4.3	0.9	0.9	0.4
	20–30	4.4	0.9	0.6	0.3
	30–40	4.6	0.9	0.2	0.1
	40–50	5.0	1.1	0.2	0.1
	50–60	5.4	1.1	0.1	0.1
	$\bar{x}$ (0–60)	4.8		0.65	

[a]Means of ammonium release rates were elevated by the high rates of two animals.

the pelagic invertebrates. In agreement with the hypothesis that kinetic release patterns are directly affected by the animal's food, but in exception to most of our data, three tubificid individuals in the flow cell at 12°C did show a decrease in excretion rate over time (Fig. 2). Two of these individuals also had exceptionally high excretion rates; initial rates of these individuals were 35 and 24 nmol NH_4 (mg AFDW)$^{-1}$·h^{-1} (Fig. 2). Other tubificids in the flow cell at 12°C (4) had excretion rates of less than 5 nmol NH_4 (mg AFDW)$^{-1}$·h^{-1}. Thus, both the rate of excretion and the relative influence of food removal can be highly variable among individual tubificids even if the animals are sampled from the same site and incubated under the same conditions. Similar variations in ammonium excretion rates were noted among individuals of the benthic marine amphipod *Corophium volutator* (Hawkins and Keizer 1982).

Because the animals were collected at two different times of the year and thus incubated at two different temperatures, the effect of season/temperature on excretion rates was considered by comparing rates at 10–12°C to rates at 22°C for each technique. Because excretion rates did not decrease significantly with time for most animals, we determined the mean excretion rate over all time intervals for each individual before making comparisons. In the static experiments, ammonium release rates of both chironomids and tubificids were significantly higher ($P < 0.05$, Mann–Whitney) at 22°C than at 12°C (Table 2). However, in the flow cell experiments, temperature did not significantly affect the ammonium release rates of either taxa. It is not clear why the two techniques gave different results regarding the influence of temperature on excretion rates. The major difference between the two techniques was the degree of animal confinement in the

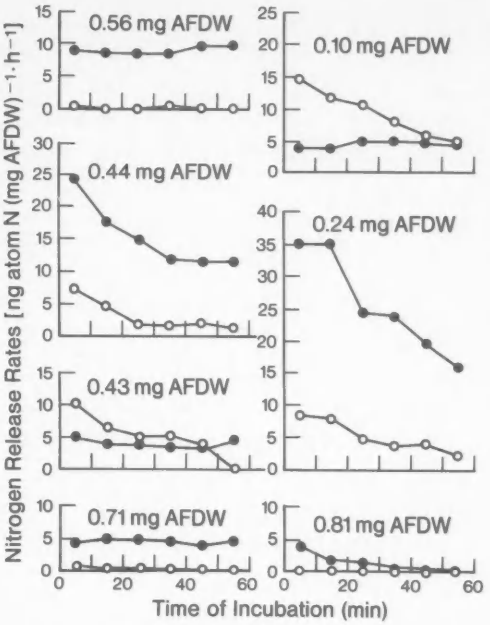

FIG. 2. Ammonium (●) and primary amine (○) release rates for seven individual tubificids during six successive 10-min intervals after the animals were removed from food (natural substrate). Animals were collected June 15, 1982, and incubated at 12°C for nitrogen release measurements.

flow cell (volume = 0.05 mL) vs. the static incubation chamber (volume = 11 mL). Metabolic changes reflecting physical activity may have been more pronounced in the static chamber than in the flow cell because the larger volume of the former was probably conducive to increases in physical activity expected at a higher temperature. Alternatively, the differences may have simply reflected differences in sampling locations. Technique comparisons were not completely valid because animals analyzed by the respective methods were collected on different days.

Primary amine release was not quantified in the long-term static incubations because of the potential for amino acid removal by microorganisms (e.g. Gardner and Miller 1981). However, assuming that microbial uptake would be minimal during the 10-min flow cell incubation intervals, we estimated the amounts of amino acid nitrogen released during the flow cell experiments. Although subject to errors because of the unknown composition of the free amino acid pool, our primary amine estimates provide an indication of the relative magnitude and patterns of amino acid nitrogen release by these animals after they were removed from their natural substrates. In contrast to the relatively constant mean ammonium release rates over time, free amino acid nitrogen decreased to 3–22% on average of that observed in the first 10-min interval (Table 3). This decrease in free amino acid nitrogen released after the animals were removed from food suggests that free amino acids could be associated with undigested material in the animals' guts, and are subsequently released as the animals clear their guts. Alternatively, if free amino acids were released by diffusion from intracellular metabolic pools, the observed decreases could have reflected decreases in sizes of the metabolic amino acid pools after food removal. The absence of measurable amounts of amino acid nitrogen in the incubation waters of some animals and the rapid reduction in levels of amino nitrogen released in the 1st hour after food removal suggests that, in contrast to ammonium, amino acid release is not a continuous metabolic process.

We believe this to be the first study quantifying ammonium and amino acid release rates for freshwater benthic invertebrates. Our ammonium release rates compare favorably with those reported for the benthic marine amphipod *C. volutator* [1.7–9.6 nmol NH_4 (mg AFDW)$^{-1}$·h^{-1}, mean 4.27; Hawkins and Keizer 1982], but are lower than those reported for pelagic zooplankton examined at similar temperatures (e.g. Lehman 1980; Gardner and Scavia 1981). The difference between benthic and pelagic invertebrates may be due to the fact that the benthic animals were larger and likely to have a slower metabolic rate than pelagic invertebrates. As mentioned previously, it may also be related to the low quality of food available to the benthos.

Mean atomic ratios of excreted inorganic N and P were calculated for chironomids and tubificids incubated at 20–22°C by combining our ammonium release data with those previously reported for inorganic phosphorus (Gardner et al. 1981). The mean N:P ratio for chironomid excretion products was 15:1 as compared to 35:1 for tubificids. The difference in mean N:P ratios between chironomids and tubificids could be due to metabolic characteristics of the respective groups or may reflect differences in the food ingested. Chironomids ingest suspended materials and surface sediments and the mean ratio for their excretion products is similar to the ratios reported for phytoplankton biomass (Goldman et al. 1979). Tubificids, on the other hand, are burrowers and ingest sediments 2–5 cm below the sediment surface. The N:P ratios for the two taxa were within the range reported for inorganic excretion products of *D. magna* exposed to a variety of feeding conditions (N:P ratios ranging from 17 to 32; Scavia and Gardner 1982). The observed ammonium release rates for chironomids and tubificids, and the high N:P ratios of their excretion materials indicate that metabolic conversion of nutrients by benthic animals is at least as important for nitrogen mineralization as for phosphorus mineralization and that it may be a dominant mechanism for regenerating nitrogen in aerobic lake sediments.

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Predation by Sharks on the Grey Seal (*Halichoerus grypus*) in Eastern Canada

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BRODIE, P., AND B. BECK. 1983. Predation by sharks on the grey seal (*Halichoerus grypus*) in eastern Canada. Can. J. Fish. Aquat. Sci. 40: 267–271.

The increase in population size of the grey seal (*Halichoerus grypus*) off eastern Canada over the past 20 yr may be attributed to a decrease in shark stocks, their supposed predators. Reduction of the shark population is presumed to have resulted from a directed longline fishery and, of greater significance, from a change in the fishery for swordfish (*Xiphias gladius*) from selective harpooning to pelagic longlining, which has produced a large bycatch of sharks. The resulting enhanced survival of grey seals is reflected in greater infestation of commercially important fish species by the codworm (*Phocanema decipiens*).

Key words: grey seals, harbour seals, sharks, swordfish, codworm, predation, fisheries

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On peut attribuer l'importance accrue de la population de phoques gris (*Halichoerus grypus*) au large de la côte est canadienne ces 20 dernières années à la diminution des stocks de requins, leurs présumés prédateurs. On croit que la diminution des populations de requins a résulté d'une pêcherie à la palangre dirigée contre ces poissons et, ce qui est plus important, d'un changement de méthode de pêche de l'espadon (*Xiphias gladius*). Cette dernière en effet a passé d'une harponnage sélectif à une pêche pélagique à la palangre, ce qui a entraîné de fortes prises secondaires de requins. Concurremment, une meilleure survie des phoques gris est accompagnée d'une plus forte infestation de poissons de commerce importants par le ver de la morue (*Phocanema decipiens*).

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OBSERVATIONS over the years indicate that predation by sharks upon marine mammals is not unusual. This was considered to be an important factor by Kenyon (1981) in the natural mortality of the Hawaiian monk seal (*Monachus schauinslandi*). Ainley et al. (1981) and Leatherwood et al. (1972) describe attacks by sharks on several species of seals and dolphins, respectively, off California. In the Bay of Fundy the white shark (*Carcharodon carcharias*) was shown by Arnold (1972) to prey on the harbor porpoise (*Phocoena phocoena*), whereas our own personal observations on Sable Island show that it also preys on the grey seal (*Halichoerus grypus*). Sharks have been considered as important predators in eastern Canada by Day and Fisher (1954), Templeman (1963), and Boulva and McLaren (1979), the latter authors with particular reference to harbor seal (*Phoca vitulina*) on Sable Island.

We discuss the past and present status of the grey seal in eastern Canada and consider the possibility that the observed increase in population size may be linked to a decline in numbers of predatory sharks, which is in turn, both a direct and indirect consequence of commercial fishing practices.

Recent History of the Shark Fishery

Prior to the directed commercial fishery for sharks, bycatches of sharks by other fisheries were insignificant owing to the types of gear used. About 18 species of shark are known to occur off Nova Scotia (Leim and Scott 1966; Tompkins 1968), of which the larger species are smooth hammerhead (*Sphyrna zygaena*), porbeagle (mackerel) (*Lamna nasus*), Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) shortfin Mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*), oceanic white tip shark (*Carcharhinus longimanus*), dusky shark (*Carcharhinus obscurus*), and white shark (*Carcharodon carcharias*).

Investigations by Aasen (1963) concluded that sharks were widespread, migrating from the Gulf of Maine to Newfoundland and, for the purpose of a fishery at that time, constituted a previously unexploited number of stocks.

Fishing was directed primarily toward the porbeagle with lesser catches of blue and mako sharks, the greatest effort taking place in the late 1950s and early 1960s through a Norwegian fishery off Nova Scotia (Aasen 1963; Tompkins 1968). As an example of the intensity of fishing effort, some 10 000 sharks were landed from March to September 1961 (Aasen 1963).

Coincident with this directed shark fishery in the 1960s was a change in technology within the fishery for swordfish (*Xiphias gladius*) in eastern Canada. The hand harpoon fishery was replaced by longlining, which allowed expansion into previously unfished areas while extending the fishing season

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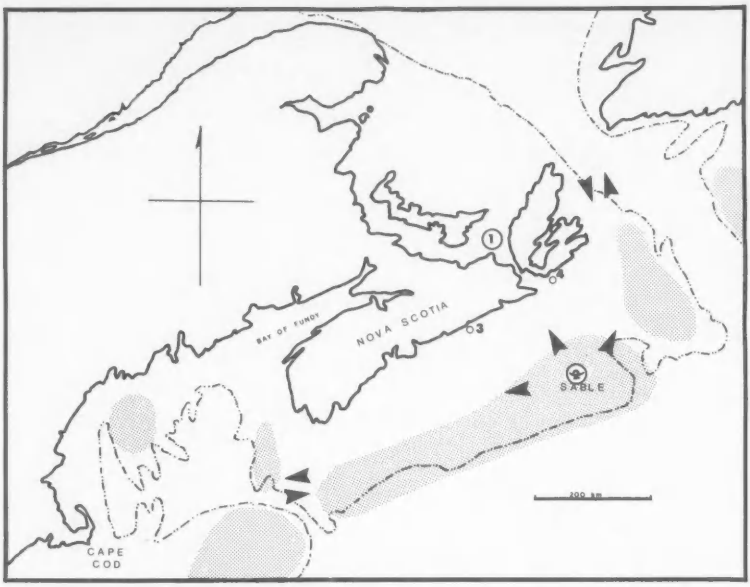

FIG. 1. General movement of grey seal juveniles (indicated by arrows) off Nova Scotia and in the Gulf of St. Lawrence from their birth sites (circled). Present pup production based on counts of individuals and (in the Gulf of St. Lawrence) supplemented with aerial and ship sightings are as follows: (1) Gulf: 3500+; (2) Sable Island: 4500; (3) Camp Island: 150; (4) Basque Island: 150. The shaded areas indicate fishing grounds where sharks were caught by a directed fishery or as significant bycatches in the swordfishery for *Xiphias*.

and resulted in increased catches (Tibbo et al. 1961; Beckett and Tibbo 1968). This fishery was no longer species selective and there were large incidental catches of sharks, in particular porbeagle, hammerhead, and mako (Tompkins 1968; personal communication with fishermen). Anderson (1979, 1980) reported that the shark bycatch was 2–3 times as great as the catch of swordfish by the fleet off the U.S. coast. The areas of both shark fishing and swordfishing are indicated in Fig. 1. Based on quantity of species caught, the swordfishing industry would have been better classified as a shark fishery with a bycatch of swordfish.

Shark catches off Nova Scotia began to decline to the point that the Norwegian fishery abandoned the fishing grounds off eastern Canada in 1964 (Tompkins 1968). The much larger longline fishery for swordfish continued to flourish with its usual bycatch of sharks until unacceptable mercury levels detected in the swordfish forced a closure of the Canadian fishery in 1971 (Anderson 1980). Longline fishing for large pelagic species such as tuna, swordfish, and sharks continued to be conducted by other countries off the Canadian and U.S. east coast, initially at reduced levels. In the late 1970s a directed fishery for sharks resumed off the east coast, this time by vessels from the Faeroe Islands. Canadian vessels have only recently been permitted to resume swordfishing.

In most fisheries shark catches, however large, were incidental; thus landings of these commercially unattractive species were probably underreported. According to Anderson (1980), the Canadian and U.S. longline fisheries in the Maine–Virginia sector landed ~42 000 t between 1962 and 1978. At the given mean weight of 41 kg (90.8 lb), slightly fewer than 1 000 000 sharks were landed during a period of 16 yr. This estimate does not include bycatches from other fisheries; however, it illustrates the magnitude of shark removals during the past two decades.

We conclude that the joint effects of directed shark fisheries and substantial shark bycatch mortality, caused by a shift of other fisheries to the use of longline technology, served to reduce the standing stocks of large shark species. We suggest that grey seal stocks experienced a much reduced mortality in consequence.

Recent History of the Grey Seal Population

Mansfield (1965) estimated the eastern Canadian population to be ~3000. Mansfield and Beck (1977) described the population as expanding, with a population of 1-yr-old and older animals of 24 000 in 1976 and annual pup production of 6400. Zwanenburg et al. (1981) concluded that the 1980 population of 1-yr-old and older animals stood at ~45 000 with pup production over 10 000 and no sign of a leveling off or decreasing trend. This rapid increase is well illustrated by the pup production on Sable Island (Fig. 2), for the period 1962–82, derived from counts made during tagging operations. Mansfield and Beck (1977) calculated that births had

increased by an average of 11.3% per annum between 1962 and 1976. From our data for the period 1976 to 1982 (Fig. 2) the annual increase appears to have increased further to 16%. The census techniques used since the mid 1960s have been comparable.

Correlation of this change with activities or events such as disturbance of small breeding colonies near the Nova Scotian coast, competition with harbor seals, and changing ice patterns in the Gulf of St. Lawrence have, to date, been difficult to demonstrate (Mansfield and Beck 1977), suggesting that other potential explanations, such as reduction of predation, should be sought to account for the rapid growth of grey seal population in the past two decades.

Since 1967 a government controlled cull of grey seals has been conducted during the January–February breeding season in all colonies with the exception of Sable Island. By 1981 a total of 13 142 seals had been taken representing an annual mean cull of 876, of which 80% were pups (Zwanenburg et al. 1981). A bounty on grey seals, excluding Sable Island, implemented in 1976 and not applicable during the breeding season resulted in a further average take of 750 adults and subadults per annum. Based on personal field experience, a conservative estimate for sinking loss associated with the bounty kill would be 50% of total kill, thus we calculate a mean annual bounty kill of 1500 and a yearly total which includes the cull of at least 2250. The cull and bounty kill appears therefore responsible for removal of less than 5% of current standing stock, a relatively insignificant rate. We now examine the possibility that large sharks are a significant grey seal predator.

Grey Seal Vulnerability to Sharks

Observation on Sable Island indicates that sharks mutilate seals (Fig. 3), and fishermen on swordfish boats have reported sighting large sharks in the shallows adjacent to seal concentrations. One fisherman provided us with jaws of sharks taken in the area which were identified as those of the porbeagle. A Sable Island resident, Mr Albin Richard (personal communication), observed a shark attack on an adult female grey seal in September 1978. The seal came ashore with its entire foreflipper and scapula removed, and died within several minutes. During May–June 1980, one of us obtained additional direct evidence of predation. Twenty-three harbour seal pups, 16 of which had been recently tagged, were killed and partially eaten by sharks patrolling the beaches. A similar event was observed in 1981 with 21 pups being killed in a single evening. The total numbers of harbour seal pups born on Sable Island in 1980 and 1981 were 325 and 366, respectively; thus the corresponding 7% and 6% mortalities of pups in this colony due to sharks over the short periods of observation underline the significance of such losses to the population. It should be noted that this is based on the number of carcasses coming ashore and cannot take into account those which may have either drifted away or were totally consumed.

While there is no doubt that seals in this region are subject to shark attacks, it is difficult to ascertain the frequency of attack and the rate of survival, especially of the younger, smaller seals. At what is assumed to be the more vulnerable

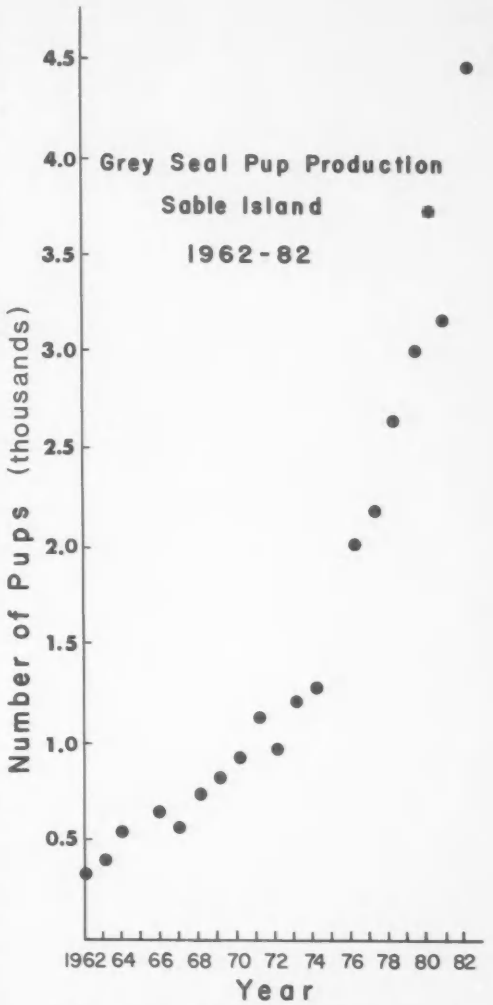

FIG. 2. Grey seal pup production on Sable Island from 1962 to 1982 based on Mansfield and Beck (1977) with additional observations to 1981.

stage of their lives, grey seals frequent areas where there is a greater exposure to sharks. At a very early age (2–3 mo) grey seals are highly active and wide ranging, as demonstrated by tagged individuals (Mansfield and Beck 1977). Observations so far suggest that younger animals tend to be more pelagic whereas the adults frequent shores of the mainland. This probably occurs because juveniles which have been born on Sable Island are already well offshore, and most of those born on the ice of the Gulf of St. Lawrence are carried out through Cabot Strait towards Sable Island before the ice deteriorates. A year-round movement, indicated by tag returns, therefore

FIG. 3. Live harbor seal (*P. vitulina*) adult with wounds from recent shark attack off Sable Island. Photo by Zoe Lucas, 1981.

appears to occur in the areas that are most abundant in sharks and swordfish (Fig. 1). If predation by sharks were a prime factor in grey seal mortality, the history of reduction of these predators by direct and indirect fisheries would be reflected in the present status of the east coast grey seal. Had the survival of juveniles begun to increase during the early 1960s, we would expect, as we now have observed, the marked increase in the numbers of breeding females in subsequent years.

Tagging studies (K. Zwanenburg and B. Beck unpublished data) so far indicate that, despite the wide-ranging habits of juveniles, most return to their original site as breeding adults. This indicates that the increase at Sable Island is real and not an artifact of immigration.

The precise degree or time scale of any response to changes in size of shark populations is difficult to determine for several reasons. Individual sharks must be of a size sufficient to attack large prey (a 50-kg juvenile seal, for example), and growth rates of sharks are slow (Aasen 1963; Anderson 1980). Thus reduced size as well as numbers of sharks in recent years may have permitted the increased survival of several year-classes of grey seals. The larger body size of adult grey seals may reduce their susceptibility to attack or, if attacked, may increase their chance of survival. It is noteworthy that shot samples of grey seals yield adults with scars from shark attacks whereas juveniles are free of scars, suggesting that escapement is low for the smaller animals.

To summarize, we assess the available evidence as follows: (1) indirect and directed fisheries have exerted significant mortalities on the stocks of large sharks of the Scotian Shelf; (2) a substantial increase in grey seal abundance over the same time period does not appear to be associated with environmental change or human activity; (3) sharks inhabit the same areas as grey seals; and (4) sharks are known to cause substantial mortality in harbor seals in the same area. Unfortunately no data exist which might provide quantitative evidence that shark predation once held grey seal abundance at low levels, and that reduced shark abundance in recent decades has reduced that controlling effect. Our case, accordingly, is circumstantial, although we believe, still compelling.

The question of why the harbor seal population on Sable Island has not shown a similar increase (Boulva and McLaren 1979) for the same reason is considered. The harbor seal is a considerably smaller species than the grey seal and probably more vulnerable to attack and with less chance of surviving. Furthermore, their May–June pupping season coincides with local abundance of sharks around Sable Island. Evidence, based on field observations, presented here would suggest that a small number of local sharks would be sufficient to inflict considerable damage on harbor seal colonies. By contrast, the grey seal pups disperse shortly after the January–February pupping season and appear to be well distributed during the summer.

A possible correlation between grey seal stock size and fluctuations in their predators through direct and indirect fisheries is, in itself, intriguing and potentially important to management intervention, but the implications for multispecies management are also important. The grey seal is of economic importance, directly through its destruction of inshore fishing gear, and indirectly as the principal vector in the life cycle of the codworm (*Phocanema decipiens*) which infests several important inshore commercial species of fish, in particular Atlantic cod (*Gadus morhua*), rendering them less marketable (Mansfield and Beck 1977; Odense 1978). If our hypothesis is correct, it underscores the complexities of multispecies management, by suggesting that the advantage of technological changes in one fishery may be partly offset by the devaluation of others.

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The Effect of Parameter Uncertainties in an Age–Length Relationship upon Estimating the Age Composition of Catches

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A simple, but frequently applied, procedure for decomposing fish length frequencies into age-classes is considered. This decomposition consists of converting fish lengths into ages using an age–length relationship. A method for assessing the effect of parameter uncertainties in this relationship upon estimates of the age composition of catches is presented. It is assumed that the parameter uncertainties can be described by probability distributions. Our aim is to determine probability distributions of age composition estimates resulting from these uncertainties. This is done using a stochastic sensitivity analysis technique involving Monte Carlo simulations and/or a first-order theory if such a theory is valid in the case under consideration. The method is illustrated by its application to data from the southern bluefin tuna (*Thunnus maccoyii*) fishery. It is found that simulated (Monte Carlo) catch estimates for age-classes 3 (fish at age 2–3 yr) to 13 (fish at age 12–13 yr) are normally distributed. The coefficients of variation of these estimates are less than 12%. Simulated catch estimates for age-classes 1, 2, and 14–20 deviate considerably from normality and their ranges bounded by the 2.5 and 97.5 percentiles are extremely wide; they include values different by up to 810% from the best deterministic catch estimates.

Key words: catch, age composition, uncertainties, sensitivity analysis, Monte Carlo simulations, southern bluefin tuna

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On trouvera dans l'article qui suit l'examen d'une méthode simple et fréquemment utilisée pour décomposer les fréquences de longueur en classes d'âge chez les poissons. Elle consiste à convertir les longueurs en âges à l'aide d'une relation longueur–âge. Nous décrivons une méthode d'évaluation de l'effet des incertitudes quant aux paramètres sur les estimations de la composition par âge des prises. Nous supposons que ces incertitudes peuvent s'exprimer par la distribution des probabilités. Nous voulons déterminer cette distribution pour les estimations de composition par âge résultant de ces incertitudes. Pour y arriver, nous utilisons une technique d'analyse de sensibilité stochastique comportant des simulations de Monte-Carlo, ou une théorie de premier ordre, ou les deux, quand une telle théorie est valide dans le cas sous étude. Nous illustrons la méthode par des données sur la pêche du thon rouge méridional (*Thunnus maccoyii*). On constate que les estimations de prises des poissons de classe d'âge 3 (entre 2 et 3 ans) à 13 (entre 12 et 13 ans) ont une distribution normale. Les coefficients de variation de ces estimations sont inférieurs à 12 %. Les estimations de prises simulées pour les classes d'âge 1, 2 et de 14 à 20 s'écartent beaucoup de la normale et leur éventail, compris entre les percentiles 2,5 et 97,5, est extrêmement large; on trouve des valeurs pouvant différer jusqu'à 810 % des meilleures estimations déterministiques des prises.

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AGE composition statistics concerning commercial catches and/or other samples of fish populations constitute the main input information required for assessing the biological state of these populations (see reviews in Gulland 1969, 1977; Ricker 1975).

If a method of fish age determination such as scale, otolith,

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vertebrae, or fin ray section reading (see reviews in Bagenel 1975; Brothers 1979; Beamish 1981; Prince and Pulos 1983) is fully validated and sufficiently efficient to allow aging large numbers of fish every year, an age−length key procedure (see Fredriksson 1934; Ketchen 1949; Tanaka 1953; Ricker 1975; Southwards 1976; Kimura 1977; Westrheim and Ricker 1978) is most appropriate for estimating the age composition of catches. This is because such estimates are only subject to sampling errors and these errors can be all but eliminated if the sampling is properly designed (see the above references). Clark (1981) proposes a computer procedure to eliminate the necessity of continuous age sampling if the distributions of fish lengths at ages represented in the catches do not change over time. However, there are many species for which the methods of reading hard part sections are at present not developed or only partly validated.

If the distributions of fish lengths at ages are approximately normal or lognormal, various graphical (e.g. Harding 1949; Cassie 1954) and computer (e.g. Hasselblad 1966; Kumar and Adams 1977; Macdonald 1969, 1975; Macdonald and Pitcher 1979) methods can be applied to estimate the age composition of a fish sample from information on the sample length composition only. Their application consists of (i) finding the number of age-classes in the sample and (ii) decomposing the length−frequency into that number of age-classes. Step (i) in the case of both kinds of methods usually requires subjective decisions to be made by the user, even in ideal cases where single age-class modes are visually distinguishable in the length frequency. The computer methods are usually superior to the graphical ones for achieving (ii), though the numerical search algorithms utilized in the computer methods cannot be guaranteed to locate the desired estimates very precisely for purely computational reasons (Clark 1981). This inaccurate estimation is likely to happen if single age-class modes are not visually distinguishable in the length frequency and the number of age-classes represented in the sample is large. Violation of the assumption of normality or lognormality, frequent in the case of fish length distributions, may also result in biased estimates of the age composition (see McNew and Sommerfelt 1978).

The subjectivity of the user's decisions may be reduced if some information on fish growth which is independent of length−frequency statistics is available. For instance, Schnute and Fournier (1980) propose a procedure which eliminates these decisions if the forms (but not necessarily the parameters) of (i) the age−length relationship and (ii) the relationship between standard deviation of length and mean length at age are known. Information on the form of relationship (ii) is especially difficult to obtain for those species for which direct aging (i.e. reading hard part sections) is not feasible. Age composition estimates from this procedure tend to be very sensitive to changes in the forms of the relationships, especially of relationship (ii) (see the above reference).

Because of the information required, the computational difficulties, and the assumptions associated, the methods for decomposing a distribution mixture into its components are not universally applicable. For example, long-living fish species having relatively long spawning periods with multiple activity peaks (e.g. most species of tunas) rarely have length frequencies which display modes representing single age-classes. As stated earlier, such length frequencies are difficult to decompose into age-classes using the distribution mixture methods. Also, the direct aging methods for these species are frequently not developed.

If the age−length relationship is known (e.g. on the basis of mark−recapture data or laboratory studies) for such a species and none of the procedures mentioned is appropriate, it is possible to decompose length-frequencies into age-classes simply by converting fish lengths to ages using this relationship (as demonstrated by Gulland 1969) and then classifying these aged fish into age-classes. This method, although crude, is frequently used for many long-living species, such as tunas and billfishes (see Gulland and Skillman 1980), e.g. Atlantic bigeye tuna, *Thunnus obesus* (Kume 1978), Atlantic northern bluefin tuna, *Thunnus thynnus* (Baglin 1977), and southern bluefin tuna, *Thunnus maccoyii* (Hayashi 1974; Skillman and Shingu 1980; Murphy and Majkowski 1981; Majkowski 1982a). As many management decisions rely on the results of this method, it was recommended by participants of an international fish stock assessment workshop to investigate its reliability (see Gulland and Skillman 1980).

The objective of this paper is to present a method for assessing the effect of parameter uncertainties in the age−length relationship upon estimates of the age composition of catches. It is assumed that the parameter uncertainties can be described by probability distributions. Our aim is to determine probability distributions of age-composition estimates resulting from these uncertainties. The method is illustrated by its application to data from the southern bluefin tuna fishery.

Method

Notation

p_j	A parameter of an age−length relationship ($j = 1, \ldots, n$)
p_j^o	The best deterministic estimate of p_j ($j = 1, \ldots, n$)
C_i^o	An estimate of the number of caught fish belonging to the ith age-class which is derived on the basis of the p_j^o values ($i = 1, \ldots, m$)
C_i	An estimate of the number of caught fish belonging to the ith age-class which is derived on the basis of perturbed values of p_j^o's ($i = 1, \ldots, m$)
D_i	A scalar function which measures differences between C_i^o and C_i (for examples see Table 1).

Background

The technique proposed for assessing the probability distribution of C_i resulting from the stochastic nature of information on p_j's is referred to, in mathematical modeling fields, as stochastic sensitivity analysis (see reviews in Majkowski 1982b, 1983). This technique, originally recommended for testing simulation models (Miller 1974a, b; Miller and Bramall 1976; Miller et al. 1976; Garten et al. 1978; O'Neill and Gardner 1979; Gardner et al. 1980; O'Neill et al. 1980; Majkowski et al. 1981a), may also be suitable for examining uncertainties in results of quantitative procedures (for an example see Majkowski and Waiwood 1981).

TABLE 1. Brief description of first-order theories.

Theory	D measure	Linear approximation	Predicted distribution	References
Additive	$D_i = \frac{C_i - C_i^o}{C_i^o}$	$D_i \cong \sum_{j=1}^{n} R_{ij} u_j$ where $R_{ij} = \frac{\partial D_i^a}{\partial u_{j\mid p_j = p_j^o}}$ and u_j is a relative change in p_j	D_i has a normal distribution with the mean equal to 0 and the variance of $\sum_{j=1}^{n} R_{ij}^2 \sigma_j^2 + 2\sum_{j<k} R_{ik}\sigma_j\sigma_k\rho_{jk}$ where σ_j^2 is the variance of p_j and ρ_{jk} is the correlation coefficient between p_j and p_k	Miller 1974a; Miller and Bramall 1976; Miller et al. 1976; Majkowski 1982b, 1983
Multiplicative	$D_i = \frac{C_i}{C_i^o}$	$\ln D_i \cong \sum_{j=1}^{n} \bar{R}_{ij} z_j$ where $\bar{R}_{ij} = \frac{\partial \ln D_i^a}{\partial z_{j\mid z_j = 0}}$, $z_j = \ln f_j$, and $f_j = \frac{p_j}{p_j^o}$	$\ln D_i$ has a normal distribution with the mean of 0 and the variance of $\sum_{j=1}^{n} \bar{R}_j^2 \bar{\sigma}_j^2 + 2\sum_{j<k} \bar{R}_{ij}\bar{R}_{ik}\bar{\sigma}_j\bar{\sigma}_k\bar{\rho}_{jk}$ where $\bar{\sigma}_j^2$ is the variance of $\ln p_j$ and $\bar{\rho}_{jk}$ is the correlation coefficient between $\ln p_j$ and $\ln p_k$	Majkowski et al. 1981a; Majkowski 1982b, 1983

[a]This value can be numerically estimated by implementing ordinary sensitivity analysis (see the First-Order Theories section) for a small perturbation level, for example, the 1% level.

The probability distribution of C_i can be determined on the basis of Monte Carlo simulations and/or with the aid of a first-order theory if such a theory is valid for the case under consideration.

MONTE CARLO SIMULATIONS

The use of Monte Carlo simulations in stochastic sensitivity analysis involves performing repeated evaluations of C_i, each time using p_j values stochastically sampled from their probability distributions. For each simulation the value of D_i is calculated. When the number of simulations is large enough, the mean and variance of D_i can be accurately estimated and histograms of D_i values analyzed (for detailed procedures see the papers cited at the beginning of the Background section).

FIRST-ORDER THEORIES

First-order theories involve linear approximations for predicting D_i values on the basis of given magnitudes of perturbation in p_j^o's (see Table 1). They are used to reduce the amount of computer time required to derive on the basis of Monte Carlo simulations all the above-mentioned information. These theories are at present formulated for two cases only, namely, if the probability distributions of p_j's are either normal (additive first-order theory) or lognormal (multiplicative first-order theory). Cross-correlations among input parameters are permissible in both cases.

Preliminary information on the validity of each of the two approximations can be obtained by implementing ordinary sensitivity analysis (for methods see Majkowski and Bramall 1980; Majkowski and Waiwood 1980, 1981). The analysis consists of calculating a number of C_i values, each derived by perturbing only one p_j^o value. It is recommended that this analysis be performed for various percentage changes within the uncertainty ranges of p_j^o's. If the approximation is valid, the relationship between the values of D_i and u_j's in the additive case or between the value of $\ln D_i$ and $\ln f_j$ in the multiplicative case should be approximately linear (see Table 1). The degree of linearity can be determined by plotting Monte Carlo simulated D_i values against those predicted by the first-order theory (Miller 1974a; Miller et al. 1976; Majkowski et al. 1981a). Usually, even a relatively small (i.e. insufficient for gaining accurate information on the probability distribution of D_i) number of Monte Carlo simulations can provide a reliable indication of whether the theory is valid or not.

Example of Application

The method is illustrated by its application to catch length-frequency data from the southern bluefin tuna fishery. Southern bluefin tuna are subject to Australian (pole and live bait fishing and purse seining) and Japanese (longlining) fisheries. Information on the biology of, and fisheries directed at, this species is documented in Murphy (1977), Shingu (1978), Majkowski et al. (1981b), and Murphy and Majkowski (1981).

METHOD OF DETERMINING C_i

The length-frequencies (1- and 2-cm length-classes are used for the Australian and Japanese catches, respectively) of caught fish are constructed on the basis of sampling informa-

TABLE 2. Characteristics of the parameters of equation (3) (Dr G. P. Kirkwood, CSIRO, Cronulla, NSW, Australia, unpublished data).

Parameter	Value	Variance−covariance matrix		
		t_o	k	L_∞
t_o [years]	−0.429	0.004		
k [years^{-1}]	0.127	0.0002	0.00002	
L_∞ [cm]	207.7	−0.12	−0.011	8.4

TABLE 3. The 1963-, 70-, and 78-catches (in numbers) decomposed into age-classes (age-class i denotes fish at age $i-1$ to i years) using the best estimates of t_o, k, and L_∞.

Age-class	1963	1970	1978
1	0	690	1 207
2	2 903	68 312	234 961
3	87 045	695 798	486 223
4	67 566	163 115	305 058
5	51 992	58 702	207 853
6	87 937	104 458	148 808
7	94 347	53 717	76 635
8	115 485	68 485	52 826
9	196 095	85 441	71 297
10	203 103	111 059	76 537
11	148 030	89 625	44 390
12	72 976	60 941	21 015
13	27 122	35 534	10 090
14	6 904	15 453	3 951
15	2 033	8 137	2 000
16	463	3 271	458
17	204	1 173	310
18	89	480	156
19	12	274	43
20	20	191	83

tion and gross catch data for, usually, consecutive half-month and year quarter periods of the Australian and Japanese fishing seasons, respectively, for each statistical subarea of the fishing grounds (see Hampton 1982a, b). The length-frequencies are then converted into age-class frequencies in the following way:

i) The age, t (in years), for fish in each length-class is estimated from the midpoint of the length class L using the von Bertalanffy age−length relationship (see Gulland 1969):

$$(3) \quad t = t_o - \frac{1}{k}\ln(1 - L/L_\infty).$$

The means and the variance−covariance matrix of the growth parameters are presented in Table 2. They were jointly estimated using a maximum likelihood method on the basis of (α) tag−recapture information (i.e. length increment at liberty period data; see Hearn 1982; Williams 1982) on 794 fish being at liberty 0.7−12.5 yr and (β) 77 age at length observations for ages up to 5 yr which are made by visual inspection of the catch length-frequencies [there are clearly defined modes corresponding to ages up to 5 yr in these length-frequencies (see Hynd 1965)].

ii) Fish are classified into cohorts according to their calculated dates of birth (the birth date is calculated by subtracting t from the midpoint of the capture period). All fish having the birth dates between July 1 of year x and June 30 of year $x + 1$ are assigned to a single cohort denoted by $x + 1$. Such an assignment is consistent with our knowledge of the spawning period (October−March) of southern bluefin tuna (see Shingu 1978).

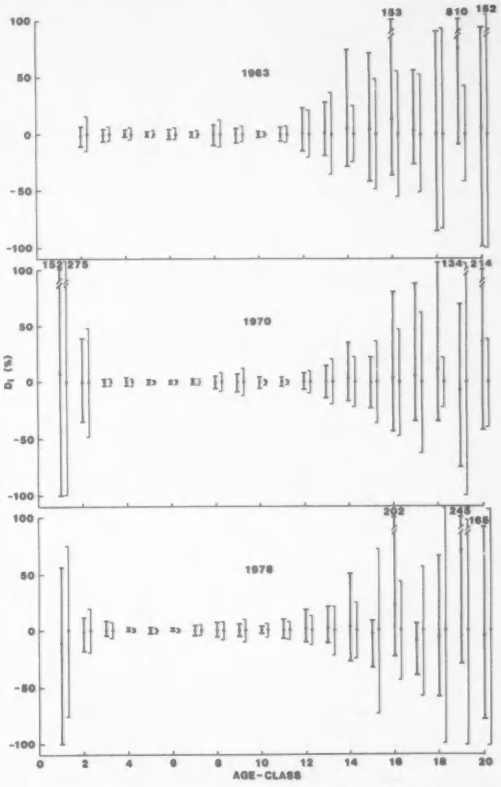

FIG. 1. The Monte Carlo simulated mean values (indicated by dots) and ranges bounded by the 2.5 and 97.5 percentiles (indicated by solid bars) of D_i, both obtained assuming a uniform distribution of lengths within each length-class. The brackets mark the above-mentioned ranges predicted by the additive first-order theory.

iii) The age-class of the fish from each length-class is defined by the difference between the year of capture increased by one and the year denoting the determined cohort (e.g. a group of fish classified into the 1976 cohort and caught during the first half of February 1980 is assigned to age-class 5).

iv) It occasionally happens that the length-class under consideration contains within it an age-class boundary. In such cases, a uniform distribution of lengths within the length-class is assumed. In this way, the catch can be apportioned between the two age-classes represented in the length-class proportionate to the exact positioning of the age-class boundary.

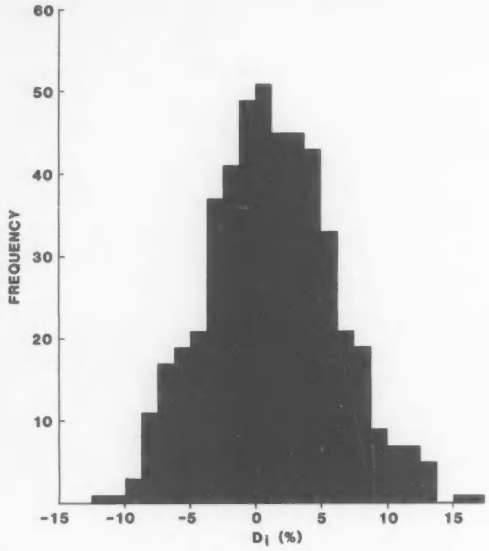

FIG. 2. A typical frequency distribution histogram of D_i for age-classes 3−13. (The histogram presented is for 1978 age-class 11.)

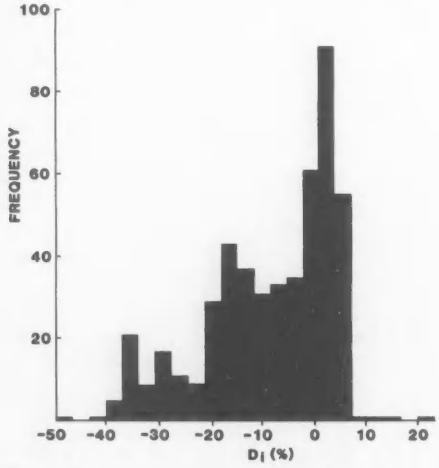

FIG. 3. A typical frequency distribution histogram of D_i for age-classes 1, 2, and 14−20. (The histogram presented is for 1978 age-class 17.)

SENSITIVITY ANALYSIS: IMPLEMENTATION AND RESULTS

Catches in 1963, 1970, and 1978 are selected for the analysis. The results of their decomposition using the best estimates of t_o, k, and L_∞ are presented in Table 3. The first D-measure defined in Table 1 is used in the analysis.

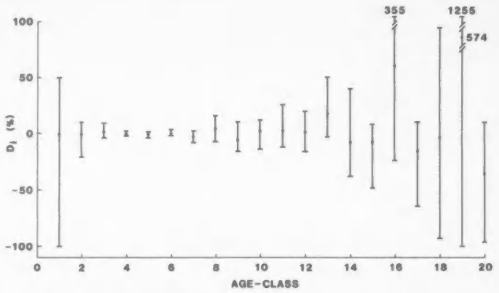

FIG. 4. The Monte Carlo simulated mean values (indicated by dots) and ranges bounded by the 2.5 and 97.5 percentiles (indicated by solid bars) of D_i for 1978, both obtained ignoring item (iv) of the description of the catch decomposition procedure.

Because the variance−covariance estimates of the growth parameters are rather small (see Table 2), it is assumed that the multivariate normal distribution defined by the values in Table 2 should closely reflect the uncertainties in these parameters (see discussion in Aitchison and Brown 1957).

Monte Carlo simulations — The results based on 500 Monte Carlo simulations are presented although a much smaller number of simulations provided information on probability distributions of D_i values as accurate as that presented. It can be observed (see Fig. 1) that the mean values of D_i's for age-classes 3−13 are relatively close to zero (the maximum difference is equal to 1.5%). Also, the ranges of the D_i values bounded by the 2.5 and 97.5 percentiles (i.e. encompassing 95% of the D_i values) are relatively narrow for these age-classes (see Fig. 1). The standard errors of D_i's (i.e. coefficients of variation of C_i's) calculated for these age-classes are less than 12%. The mean values of D_i's for the remaining age-classes deviate considerably from zero (the maximum difference is equal to 75%). Also, the above-mentioned ranges are usually much wider for the remaining age-classes; they include D_i values of up to 810%.

The examination of histograms of the D_i values obtained on the basis of Monte Carlo simulations leads to the conclusion that most statistical distributions of the D_i values for age-classes 3−13 are approximately normal (Fig. 2). The distributions for the remaining age-classes deviate considerably from normality (Fig. 3).

The correlation coefficients between the values of D_i for different age-classes were calculated for the years under consideration (they are not presented in the paper). It was observed that the D_i values for different age-classes are strongly correlated, especially those for 'close' age-classes. This could be expected considering the method of estimating C_i's.

It is of interest to mention that D_i values were also simulated ignoring item (iv) of the description of the catch decomposition procedure. The ranges of the D_i values obtained on the basis of 500 Monte Carlo simulations bounded by the 2.5 and 97.5 percentiles (for example see Fig. 4) are in this case considerably wider than those presented in Fig. 1. This comparison clearly indicates the superiority of the catch decom-

TABLE 4. The values of D_i for 1978 resulting from various perturbations in t_o, k and L_∞. (The magnitudes of the largest negative and positive perturbations for each parameter slightly exceed those determined by standard errors.)

Age-class	Parameter perturbed	Magnitude of perturbation			
	t_o	−20%	−1%	1%	20%
1		−100.0	−3.0	3.8	80.5
2		−26.2	−1.1	1.1	19.6
3		9.7	0.4	−0.4	−6.5
4		2.6	0.1	−0.1	−2.3
5		−3.0	−0.1	0.1	2.1
6		3.0	0.1	−0.1	−2.3
7		5.8	0.3	−0.3	−6.5
8		−2.5	−0.2	0.2	4.5
9		−1.0	−0.0	0.0	1.1
10		2.2	0.1	−0.1	−2.3
11		5.7	0.3	−0.3	−6.1
12		7.4	0.3	−0.3	−6.7
13		5.7	−0.3	0.3	−5.4
14		12.4	0.5	−0.5	−11.4
15		3.7	0.2	−0.2	−3.4
16		15.0	0.6	−0.6	−13.5
17		4.8	0.3	−0.3	−7.3
18		7.4	0.3	−0.3	−6.3
19		−20.6	1.0	1.0	20.8
20		12.5	0.6	−0.6	−12.4
	k	−5%	−1%	1%	5%
1		−100.0	−19.3	14.1	91.8
2		−34.1	−5.1	4.8	25.8
3		10.3	1.8	−1.6	−7.4
4		4.1	0.1	−0.2	−1.7
5		−15.6	−1.6	1.4	8.6
6		8.1	0.7	−0.6	−6.0
7		24.6	2.7	−3.4	−19.4
8		−9.0	−3.0	4.2	25.0
9		−11.4	−1.6	1.5	12.0
10		2.5	1.3	−1.3	−15.2
11		31.8	4.8	−5.2	−26.2
12		50.0	6.9	−6.5	−30.0
13		47.6	6.2	−5.6	−36.8
14		90.8	14.4	−13.6	−39.8
15		26.6	5.0	−4.1	−57.2
16		248.9	21.6	−18.1	−25.6
17		−0.1	5.6	−11.0	−44.2
18		62.6	7.0	−10.0	−70.7
19		227.4	−15.8	36.4	90.8
20		50.8	21.9	−21.5	−78.3
	L_∞	−2.5%	−1%	1%	2.5%
1		−92.6	−31.6	20.3	51.7
2		−20.8	−8.1	6.6	15.7
3		6.4	2.7	−2.0	−4.2
4		2.0	0.4	−0.3	−0.9
5		−11.0	−3.3	2.9	7.4
6		3.3	0.7	−0.6	−2.6
7		17.1	4.9	−6.3	−15.9
8		−11.3	−6.2	9.6	26.6
9		−13.2	−6.0	6.4	15.8
10		−5.9	1.0	−4.2	−13.9
11		29.0	11.7	−11.0	−27.3
12		53.3	19.1	−15.3	−34.8
13		52.8	21.0	−17.0	−46.6
14		106.9	43.9	−30.7	−43.5
15		72.6	8.8	−32.9	−77.5
16		302.0	133.0	−21.0	−44.3
17		132.8	−5.5	−40.5	−71.5
18		59.6	27.7	−60.4	−36.8
19		315.5	155.9	124.5	−85.3
20		227.6	48.8	−78.3	−86.0

position procedure described in the Method of Determining C_i section to one which ignores item (iv) of that description. The latter procedure is not considered in the following sections.

Additive first-order theory — Examination of the validity of the additive first-order theory is initiated by ordinary sensitivity analysis. The results of this examination for 1978 are presented in Table 4. Several observations can be made.

i) The D_i measure is a nonlinear function of magnitudes of perturbations in the growth parameters. The degree of deviation from linearity is quite considerable even for changes in the growth parameters within the region specified by the standard errors for these parameters. This introduces some doubts regarding the usefulness of the additive first-order theory in the case under consideration.

ii) For any fixed perturbation magnitude, the catch estimates are more sensitive to changes in k and L_∞ than to those in t_o.

iii) The catch estimates of the first few youngest and oldest age-classes are usually more sensitive to perturbations than those of intermediate age-classes. Very similar conclusions were reached when the catches for 1963 and 1970 were analyzed.

The validity of the additive first-order theory was further tested by plotting the D_i values obtained on the basis of Monte Carlo simulations against those predicted by the theory. These plots clearly indicated that this theory is not valid in the case under consideration; the points were widely scattered, not reflecting any linear relationship.

Had the additive first-order theory proven valid, the earlier introduced ranges of the D_i values would be approximately equal to the intervals $[-2\sqrt{\text{var}\,(D_i)},\ 2\sqrt{\text{var}\,(D_i)}]$, where var (D_i) is calculated according to the variance formula associated with the additive first-order theory (see Table 1). A significant disagreement between the ranges obtained on the basis of Monte Carlo simulations and the first-order theory for age-classes 14−20 (see Fig. 1) confirms that this theory is not applicable in this case. Also, the mean values of D_i's derived from the Monte Carlo simulations are frequently different from the values predicted on the basis of the theory (see Table 1).

INTERPRETATION OF RESULTS

The uncertainties identified in the C_i estimates for i equal

to 1, 2, and 14–20 are unlikely to be acceptable. Let us consider, for example, a specific but frequent use of C_i estimates. Estimates of the catch per unit of fishing effort are often used for the detection of year-to-year changes in recruitment to a fishable stock (see Gulland 1969, 1977; Ricker 1975). Based on our analysis it can be concluded that estimates of the catch per unit of fishing effort for southern bluefin tuna age-classes 1 or 2 should not be used as an index of recruitment.

The dependence of C_i variability on age-class is determined by the probability distributions of t_o, k, and L_∞, the form of age–length relationship, and the fish length-frequencies. The increase in the variance of C_i as i increases is caused by (i) a reduction in the growth rate of southern bluefin tuna with increasing age, (ii) the length-dependent predictive power of the age–length relationship (the uncertainty in the predictions of ages from lengths increases towards the extremes of the length range), and (iii) an increase in the overlap of length distributions of adjacent age-classes with increasing age. In addition to (ii), causes of the high uncertainties in C_i for the two youngest age-classes may include the size selectivity of the fishing method used, and the small catches of these fish. As a result of these, the length distributions of young fish caught may be different from those of fish in the entire population. In addition, the length frequencies of the two youngest age-classes may be subject to large sampling error, this being a consequence of the small catches (catches are sampled randomly). Similar factors can also affect to some extent the catch estimates of fish over 13 yr old.

The variance–covariance estimates of t_o, k, and L_∞ reflect errors in the data set used for the estimation of these parameters. The unsuitability of the form of age–length relationship and variabilities in the growth rate from fish to fish, year to year, and even area to area are also reflected in the variance–covariance estimates. Hence, it can be presumed on the basis of our analysis that error introduced to the catch estimates for age-classes 3–13 due to not accounting for these variabilities in the decomposition procedure is not large. This conclusion can be verified when a direct aging method is developed for southern bluefin tuna allowing the precise determination of these variabilities.

It should be realized that not all sources of error in the age composition estimates were accounted for in our analysis. These estimates can also be affected by errors in the length frequencies and a presumably small degree of unsuitability of the age–length relationship which is not reflected in the variance–covariance estimates of the growth parameters. Examination of these effects is beyond the scope of this paper.

Discussion

The example presented provides an indication of the usefulness of stochastic sensitivity analysis for assessing the reliability of catch age composition estimates derived with the aid of an age–length relationship. Such assessments will result in a greater awareness of weaknesses of these estimates and, consequently, more thoughtful use of them.

In the example presented, the variance–covariance estimates of the growth parameters reflect errors in the data set used for the estimation of these parameters, the unsuitability of the form of age–length relationship, and individual, temporal, and geographical variabilities in the growth rate. Therefore, the estimated C_i uncertainties reflected all these influences. In many cases, however, variance–covariance estimates of growth parameters may fully reflect only the first two factors (e.g. if the variance–covariance estimates are derived on the basis of laboratory studies). In such a case, caution should be exercised in optimistic interpretation of sensitivity analysis results. Also, as discussed in the Interpretation of Results section, it should be borne in mind that errors in the length-frequencies are not reflected in estimates of C_i uncertainties, which are derived as described in this paper.

The cost, in terms of computer time, of the use of the technique is not high. For example, 500 Monte Carlo simulations for each of the 3 yr and the calculations of means, standard errors, and correlation coefficients required less than 60 s of central processing time when run as a batch job on a CYBER 7600 computer system. This cost could be reduced if the first-order theory is applicable. In such a case, the distributions of D_i's could be evaluated on the basis of this theory instead of having to execute the large number of Monte Carlo simulations.

The degree of applicability of the first-order theories for assessing the reliability of C_i estimates, in general, is difficult to predict; more cases have to be examined before any generalizations can be made. These theories have proved to be quite useful in testing nonlinear simulation models (see reviews in Majkowski 1982b, 1983) although there are models for which they are not applicable (for example, see Miller et al. 1976).

If a first-order theory is applicable, comparing magnitudes of the components of the summations in the variance formula in Table 1 can provide some insight into the relative contributions of each of the variances and covariances of p_j^o's to the variance of D_i in the additive case or of ln D_i in the multiplicative case (for detailed methods see Miller 1974a; Miller and Bramall 1976; Majkowski et al. 1981a). If neither of the first-order theories is applicable to the system being studied, this insight can be gained by performing the Monte Carlo simulations with reduced magnitudes of variances and covariances of p_j's. However, this method may be expensive because many possibilities may have to be tested.

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Canola Meal in Rainbow Trout (*Salmo gairdneri*) Production Diets[1]

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HARDY, R. W., AND C. V. SULLIVAN. 1983. Canola meal in rainbow trout (*Salmo gairdneri*) production diets. Can. J. Fish. Aquat. Sci. 40: 281–286.

Production diets containing up to 20% canola meal were fed for 108 d to rainbow trout (*Salmo gairdneri*) to evaluate the effects on weight gain, food conversion, thyroid function, and organoleptic quality of market-sized fish. Weight gain was not affected by dietary canola meal level. Food conversion values and organoleptic properties were not influenced by dietary treatments. Feed costs were reduced by $18.70 (U.S.) per metric ton compared to control diet at the highest level of dietary canola meal (20%). Thyroid function was significantly affected by dietary canola meal. Dose-related changes in the histological appearance of the thyroid and alterations of plasma thyroxine and 3,5,3′-triiodothyronine levels indicated that compensatory adjustments in thyroid function allowed normal growth to proceed in the canola-fed fish. Possible mechanisms of dietary glucosinolate influence on thyroid function are discussed and areas for future research are suggested.

Key words: canola meal, plasma T_4, plasma T_3, thyroid histology, goitrogen, glucosinolates, trout growth, food conversion, least-cost diets, organoleptic quality

HARDY, R. W., AND C. V. SULLIVAN. 1983. Canola meal in rainbow trout (*Salmo gairdneri*) production diets. Can. J. Fish. Aquat. Sci. 40: 281–286.

On a offert à des truites arc-en-ciel (*Salmo gairdneri*) des rations de production contenant jusqu'à 20 % de farine de canola pendant 108 jours en vue d'évaluer les effets sur le gain pondéral, la conversion des aliments, la fonction thyroïdienne et la qualité organoleptique des poissons de taille marchande. Le gain pondéral n'est pas influencé par le niveau de farine de canola. La conversion des aliments et les propriétés organoleptiques des poissons ne sont pas, elles non plus, affectées par les traitements. Au niveau maximal de farine de canola (20 %), les coûts de la nourriture sont réduits de 18.70 $(U.S.) par tonne métrique par rapport aux régimes témoins. La fonction thyroïdienne est nettement influencée par la farine de canola. Des changements de l'aspect histologique de la thyroïde et des altérations de la thyroxine plasmatique et des niveaux de 3,5,3′-triiodothyronine liés à la dose indiquent que, grâce à des ajustements compensatoires dans la fonction thyroïdienne, les poissons nourris à la farine de canola ont une croissance normale. Nous analysons les mécanismes possibles de l'influence glucosinolate alimentaire sur la fonction thyroïdienne et suggérons des domaines de recherche future.

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CANOLA is the new name for rapeseed meal made from varieties of rapeseed developed by plant breeders to contain low levels of glucosinolates and erucic acid (Rapeseed Association of Canada 1978). Canola meal must be processed with moist heat to inactivate a naturally occurring enzyme, myrosinase. Myrosinase hydrolyzes glucosinolates, and one of the hydrolytic products is goitrin, a compound which can alter thyroid function in trout and salmon (Higgs et al. 1979). With these improvements, canola meal is an attractive food ingredient for consideration in least-cost diet formulation for trout.

Canola and rapeseed meals have previously been used in trout and salmon diets with varying success. Yurkowski et al. (1978) found that young rainbow trout (*Salmo gairdneri*) grew better when fed some diet formulations containing canola meal than they did when fed other formulations containing the same level of canola meal combined with other ingredients. Higgs et al. (1982) demonstrated that young chinook salmon (*Oncorhynchus tshawytscha*) fed a dry diet containing 16–20% canola meal grew well, but had a compensatory increase in thyroid activity as determined by histological criteria. Dietary canola meal levels of 30% resulted in significant growth reduction.

This study was designed to evaluate the effect of canola meal level in least-cost formulated trout diets on weight gain, food conversion, thyroid function, and organoleptic quality in a production-scale trout culture operation. Feeding rates and rearing densities similar to those used in commercial trout

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TABLE 1. Composition of the experimental diets.

Ingredients (%)	Dietary treatments				
	1	2	3	4	5
Herring meal	26.50	26.50	26.50	26.50	26.50
Soybean meal	25.00	15.00	10.00	25.00	25.00
Canola meal	—	10.00	15.00	15.00	20.00
Blood meal	10.00	10.00	10.50	3.64	2.05
Wheat middlings	31.14	31.29	30.84	22.35	16.84
Herring oil	6.35	6.20	6.15	6.50	6.60
Trace mineral premix[a]	0.10	0.10	0.10	0.10	0.10
Vitamin premix[b]	0.40	0.40	0.40	0.40	0.40
Choline chloride (50%)	0.18	0.18	0.18	0.18	0.18
Ascorbic acid	0.08	0.08	0.08	0.08	0.08
Pellet aid XP-4	0.25	0.25	0.25	0.25	0.25

[a]Trace mineral premix contained the following per kilogram of premix: 184.8 g $ZnSO_4$, 206.8 g $MnSO_4$, 49.5 g $FeSO_4 \cdot 7H_2O$, 3.85 g $CuSO_4$, 0.836 g KIO_3.

[b]Vitamin premix contained the following per kilogram of premix: 26.4 g D-calcium pantothenate, 7.7 g pyridoxine-HCl, 13.2 g riboflavin, 55 g niacinamide, 2.2 g folic acid, 8.8 g thiamin mononitrate, 88 mg biotin, 5.5 mg vitamin B_{12}, 2.75 g menadione sodium bisulfite complex, 88 000 I.U. DL-alpha tocopheryl acetate, 110 000 I.U. vitamin D_3, and 1 650 000 I.U. vitamin A palmitate or acetate.

culture were chosen for this experiment to determine if the use of canola meal in trout diets was economically feasible.

Materials and Methods

Diet Formulation and Manufacture

Five dietary treatments were used in this experiment, one control diet and four experimental diets (Table 1). The control diet (diet 1) was the U.S. Fish and Wildlife Service trout diet formulation GR4-30. The experimental diets were variations of the control diet in which soybean meal was replaced by commercial Canadian canola meal at several levels of substitution. In diets 2 and 3, canola meal was included at 10 and 15% whereas soybean meal was limited to 15 and 10%, respectively, with restrictions placed on the other dietary ingredients. Minor adjustments in the levels of wheat middlings, blood meal, and herring oil were made to maintain the nutrient specifications of the diets (Table 2). A computer programmed for least-cost diet formulation (Computone Systems Inc., One Dunwoody Park, Atlanta, GA 30338) was used to obtain the formulations of diets. Ingredient restrictions were modified to obtain the least-expensive diet formulations within certain ingredient level limits. In diet 4, the lower and upper dietary level ingredient restrictions used by the computer were 15–25% soybean meal, 0–15% canola meal, 10–40% wheat middlings, and 0–10% blood meal. In diet 5, the upper level of canola meal was increased to 20%. The other ingredients were restricted to the same lower and upper levels as in diet 4.

The diets were steam-pelleted into $\frac{3}{16}$ in. (1 in. = 25.4 mm) pellets by a local feed manufacturing company at the start of the experiment and stored in sacks at room temperature until used. About 1000 kg of each diet formulation was made.

Fish Feeding Experiment

The feeding experiment was conducted at the Seward Park Experimental Trout Hatchery, University of Washington, Seattle, WA. About 20 000 rainbow trout, mean weight = 105 ± 6 g, were randomly distributed into five 12-m ID concrete, circular ponds. Each pond received Lake Washington water at a rate of 645 L/min. Water temperatures increased from 12 to 17°C during the 108-d experiment. After 60 d, the number of fish in each pond was reduced from 4000 to 2500 to prevent overcrowding.

The fish were hand-fed 2% body weight per day in two feedings, 6 d per week. At the start of the experiment, and every 28 d thereafter, the weight of the fish in each pond was determined by weighing 15 lots of 10 trout each. The weight gain, food conversion, and percent gain for each treatment group were then calculated.

Thyroid Function

At the end of the experiment (108 d), blood samples were obtained at noon by cardiac puncture of 10 fish from each dietary treatment, except fish fed diet 3 which had the same level of canola meal as diet 4. Plasma was analyzed for thyroxine (T_4) and triiodothyronine (T_3) levels by specific radioimmunoassays (Dickhoff et al. 1978, 1982).

Seven fish from each of dietary treatments 1, 2, 4, and 5 were killed and samples of the subpharyngeal area containing the thyroid follicles were removed and fixed. The fixative was a modification of that of Hawkes and Stehr (1980), the only modification being the omission of acrolein (0.5%). Acrolein is not necessary for good fixation of specimens taken for light microscopy (K. Stehr, Northwest and Alaska Fisheries Center, Seattle, WA, personal communication). Samples were embedded in paraplast (mp = 56°C), and 5-μm sections were removed and stained with periodic acid–Schiff reagent (Culling 1974). An index of thyroid activity was obtained for each fish by measuring thyroid follicle epithelial cell height at five separate locations in five randomly selected follicles (Higgs 1976). Only intact cells with clearly defined margins

TABLE 2. Nutrient composition of the experimental diets.[a]

Ingredients	Dietary treatments				
	1	2	3	4	5
Crude protein, %	42.10	41.10	41.10	41.00	41.00
Crude fat, %	10.00	10.00	10.00	10.00	10.00
Crude fiber, %	2.20	3.10	3.60	3.70	4.10
Metabolized energy (Kj/kg diet)	13 108	12 916	12 849	13 539	13 724
Amino acids (%)					
Arginine	2.83	2.68	2.62	2.82	2.83
Lysine	3.08	2.94	2.91	2.81	2.75
Methionine	0.78	0.78	0.79	0.82	0.83
Cystine	0.56	0.53	0.52	0.51	0.50
MET + CYS	1.34	1.31	1.31	1.3	1.34
Tryptophan	0.52	0.49	0.49	0.49	0.49
Histidine	1.23	1.21	1.22	1.15	1.14
Leucine	3.72	3.61	3.61	3.34	3.22
Isoleucine	1.68	1.56	1.50	1.76	1.79
Phenylalanine	2.04	1.95	1.93	1.87	1.84
Tyrosine	1.04	0.98	0.95	1.16	1.20
PHE + TYR	3.08	2.93	2.88	3.03	3.04
Threonine	1.70	1.68	1.68	1.76	1.79
Minerals					
Calcium, %	0.767	0.814	0.838	0.839	0.864
Phosphorus-total, %	0.928	0.975	0.977	1.026	1.057
Zinc, mg/kg	182.00	184.00	184.00	178.00	176.00
Iron, mg/kg	455.00	462.00	483.00	248.00	197.00
Glucosinolate content[b] (g 3-butenylisothiocyanate equivalents/g diet)	40.00	230.00	—	310.00	340.00
3-butenyl[c]	0.09	0.63	—	0.88	1.02
4-pentenyl[c]	0.03	0.30	—	0.45	0.51
2-hydroxy-2-butenyl[c]	0.11	0.80	—	1.15	1.33
2-hydroxy-4-pentenyl[c]	0.12	0.28	—	0.24	0.19
3-indolylmethyl[c]	ND[d]	ND	—	0.07	0.06
1-methoxy-3-indolylmethyl[c]	ND	0.36	—	0.64	0.70

[a]All values except glucosinolates are calculated concentrations.
[b]Sum of 3-butenyl, 4-butenyl, 2-hydroxy-3-butenyl, and 2-hydroxy-4-pentenyl glucosinolate × 113.
[c]Micromoles per gram diet.
[d]ND = not detectable.

and with visible nuclei were used for analysis.

PRODUCT QUALITY

Ten fish from each dietary treatment (except diet 3) were used to determine percent dressed weight and organoleptic characteristics. Dressed weight is wet weight minus viscera. Organoleptic characteristics were determined by a trained taste panel on 100-g trout steaks cut from individual fish between the pectoral and pelvic fins. The steaks were placed in sealed aluminum pans and steamed at 100°C for 30 min. Samples were scored by panelists for odor, flavor, texture, and acceptability on a 9-point hedonic scale (Babbitt et al. 1974).

One-way analysis of variance was done on the data for final weight, plasma T_4 and T_3 concentrations, thyroid epithelial cell height, and organoleptic properties (Steel and Torrie 1960). Duncan's New Multiple Range Test was used to determine significant differences between treatment mean values.

Results

FISH FEEDING STUDY

The level of canola meal in the diet of rainbow trout did not significantly affect weight gain or food conversion values in this study (Table 3). Final weights of trout fed diets 2, 3, and 5, containing 10, 15, and 20% canola meal, respectively, did not differ significantly ($P > 0.05$) from the mean final weight of trout fed the control diet. However, trout fed diet 4 (15% canola meal) were significantly smaller at the end of the experiment ($P < 0.05$) and had higher food conversion values than did fish in the other dietary treatments. Fish fed diet 4 did not feed well at the start of the experiment. Mortality of fish fed diet 4 during the 1st month was 1.2% compared to less than 0.4% for fish in the other dietary treatments. Mortality was less than 0.4% during the remainder of the experiment for all groups. The percent weight gain of fish in treatment 4 was lower than the other groups during the 1st

TABLE 3. Average final weight, percent weight gain, and food conversion for the fish fed the experimental diets for 108 d.

Diet no.	Final fish weight (g)[a]	Weight gain (g)	Weight gain (%)	Food conversion[b]
1	311.5±9.0A	209.7	206	1.74
2	322.5±8.7A	215.0	192	1.58
3	341.3±17.4A	234.0	202	1.78
4	275.1±7.1B	174.1	176	2.00
5	334.7±16.9A	230.9	222	1.65

[a]Means ± SE followed by the same letter are not significantly different ($P > 0.05$).
[b]Food fed (g)/weight gain (g).

month of the experiment, but was not significantly different during the remainder of the experiment.

THYROID FUNCTION

At each level of substitution of canola meal into the diet, thyroid tissue showed evidence of increased activity. Mean thyroid follicle epithelial cell height was significantly increased ($P < 0.05$) in trout fed 10−20% canola meal compared to trout fed the control diet (Table 4), although marked hypertrophy or hyperplasia were not observed in trout fed diets containing canola meal. The thyroid of the fish fed the control diet appeared histologically normal and similar to that described by Gaylord and Marsh (1912), generally with squamous to low cuboidal follicular epithelium, few mitotic figures, nuclei oriented parallel to the basal lamina, and abundant colloid. Thyroid follicles of fish fed the 20% canola meal diet (diet 5) displayed a low to high cuboidal epithelium with some cell nuclei enlarged and oriented parallel to the radial axis of the follicle. Trout fed diet 5 generally displayed no evidence of colloid depletion, with the exception of two fish which had columnar epithelium and depleted colloid. The thyroid structure of fish fed the 10 and 15% canola meal diets (diets 2 and 4) appeared to be intermediate to that of the fish fed the control and 20% canola meal diet.

Plasma T_4 levels were significantly higher ($P < 0.05$) in fish fed diets 4 and 5 (15 and 20% canola meal) compared to trout fed diet 2 (10% canola meal). However, the plasma T_4 levels of trout fed the control diet were not significantly different from the plasma T_4 levels of trout fed any of the experimental diets. Plasma T_3 levels of trout fed diets containing 10 and 15% canola meal were significantly lower than the plasma T_3 levels of trout fed either the control diet or the diet containing 20% canola meal.

No significant correlations ($P > 0.05$) were found between final weight and epithelial cell height, plasma T_4 level, or plasma T_3 level for trout fed the different diets.

PRODUCT QUALITY

Percent dressed weight did not change with increasing dietary levels of canola meal (data not shown). The weight of the viscera was about 12% of the wet weight of trout which were fed diets 2, 4, and 5, and 17% of the control fish.

The level of canola meal in the diet did not influence the organoleptic properties of the trout: trout fed the control diet scored consistently, but not significantly ($P > 0.05$), higher in odor, flavor, texture, and overall acceptability (Table 5).

Discussion

In this study, fish fed diets containing up to 20% canola meal had weight gains statistically similar to those of fish fed a control diet. These findings agree with those of Yurkowski et al. (1978), who observed that inclusion of 22% rapeseed meal in a control diet for rainbow trout by replacement of soybean meal did not depress growth. Yurkowski et al. (1978), however, found reduced weight gains when trout were fed a diet in which rapeseed meal and soybean meal were the sole protein sources. As they point out, their diets were not formulated to be isonitrogenous or isocaloric. Thus assessment of the nutritional value of canola meal in a trout diet was confounded by differences in protein and energy levels of the diets. In our experiment, the diets were formulated to be isonitrogenous and isocaloric, and no growth reduction was seen. Because of low feeding levels, the growth rates and food conversion values reported by Yurkowski et al. (1978) were lower than those normally observed in commercial trout culture. In our study, the feeding rates and rearing densities were maintained at levels similar to those used in commercial trout culture to assess the practical significance of feeding diets containing canola meal. At each level of canola meal use, feed costs were reduced compared to the control diet (1980 prices). The largest feed savings were for diet 5 (20% canola meal), where the feed cost was reduced by $18.70 U.S. per metric ton. As food conversion values and product quality were unaffected by dietary canola meal level, the reduction in food

TABLE 4. Plasma thyroxine (T_4) and triiodothyronine (T_3) concentrations and mean thyroid follicular epithelial cell height of fish fed the experimental diets.

Dietary treatment	Glucosinolate level[a]	Plasma T_4 (ng/mL)[b]	Plasma T_3 (ng/mL)[b]	Ratio T_3/T_4	Mean epithelial cell height (μm)[b]
1	40	7.9±0.5AB	6.0±0.2A	0.76	2.6±0.04A
2	230	7.0±0.7B	3.9±0.2B	0.56	3.9±0.09B
4	310	10.3±0.5A	4.0±0.5B	0.39	5.5±0.18D
5	340	9.4±0.6A	6.0±0.5A	0.64	4.3±0.10C

[a]Grams 3-butenylisothiocyanate equivalents/g diet.
[b]Means ± SE followed by the same letter are not significantly different ($P > 0.05$).

costs translated into a savings of ~3.3 cents per kilogram of trout produced.

Higgs et al. (1982) observed a reduction in the percent lipid in the body of chinook salmon fed a canola meal containing diet compared to a control diet. In the present experiment, the percent dressed weights of the trout fed diets containing canola meal were higher than that of the fish fed the control diet. Whether this represents a reduction in visceral fat in trout fed canola meal diets or is an artifact caused by the differences in whole body weight of the samples chosen is unclear.

Canola meals may contain several glucosinolates whose hydrolytic products can suppress the thyroid function. In vertebrates, dietary rapeseed can induce thyroid hypertrophy, reduced levels of intrathyroidal iodothyronines, depressed plasma-protein-bound iodide or thyroxine titers, altered affinity of plasma albumin for thyroxine, depressed growth, feed intake, and feed utilization, and histopathological changes in the liver, kidney, and thyroid (Higgs et al. 1979). Thyroid hormone synthesis and peripheral monodeiodination of thyroxine (T_4) to 3,5,3′-triiodo-L-thyronine (T_3) may also be impaired (Higgs et al. 1982, 1979; Yurkowski et al. 1978). T_4 is largely regarded as a less active precursor or "prohormone" for T_3, and up to 70% of circulating T_4 may be converted to T_3 in trout (Eales 1977). In mammals and in teleosts, the primary action of thyroid hormones is thought to be exerted at the nuclear level, where receptors in the nuclei of target cells bind T_3 with 10 times the affinity of T_4 (Bernal and DeGroot 1980; Darling et al. 1983). Impairment of either T_4 synthesis or of peripheral deiodinase activity (DEI) has the potential to result in a hypothyroid condition. An adequate thyroid status is required for normal growth and development of fishes, and the studies of Yurkowski et al. (1978) demonstrate that glucosinolate-induced histological aberrations of the thyroid of rainbow trout may be accompanied by reduced levels of plasma T_4 and by concomitant depression in growth rate.

In our study, dietary levels of 10 or 20% canola meal (diets 2 and 5) did not affect weight gain, food conversion, or plasma T_4 levels. Plasma T_3 and T_4 concentrations were maintained in all dietary treatment groups within the physiological range observed for this species when using this assay (W. Dickhoff, University of Washington, personal communication).

Mean thyroid follicle epithelial cell height (TECH) was increased in all groups receiving canola meal diets, but this was not associated at the end of the study with reduction of plasma T_4 concentration. A simultaneous decrease in plasma T_3 concentration and in T_3/T_4 ratio was noted in fish receiving diets 2 and 4. These results may have stemmed from impairment of thyroid hormone synthesis and of T_4 to T_3 conversion at peripheral sites. However, the maintenance of normal growth and of normal T_4 levels by fish fed diets 2 and 5 (10 and 20% canola meal) indicates thyroidal compensation for any effects of dietary glucosinolates on the synthesis of thyroid hormones or the peripheral deiodination of T_4. Such compensation has been suggested by other investigators (Yurkowski et al. 1978; Higgs et al. 1979, 1982). These results indicate that under practical culture conditions canola meal can comprise up to 20% of the diet of rainbow trout of this size for as long as 108 d without exceeding the capacity of the thyroid to compensate for dietary glucosinolate content. This finding corroborates the observations that rapeseed meal may comprise up to 22% of the diet for rainbow trout (Yurkowski et al. 1978), coho salmon (*Oncorhynchus kisutch*) (Higgs et al. 1979), and chinook salmon (Higgs et al. 1982) without reducing growth or plasma T_4 concentrations, although thyroid hypertrophy or hyperplasia may result at higher levels of substitution. The observation of Higgs et al. (1982) showing that adequate thyroidal compensation can be expected at dietary glucosinolate concentrations of less than 300 μg/g diet is also corroborated. However, the suitability of using canola meal in diets for longer periods or in fry or broodstock diets is still not known.

TABLE 5. Average organoleptic qualities of trout fed the experimental diets[a] (± SEM).

Diet	Odor[b]	Flavor[b]	Texture[b]	Desirability[b]
1	7.7±0.7	7.5±0.3	7.3±0.6	7.3±0.6
2	6.8±0.7	6.3±0.6	5.8±0.9	6.3±0.6
4	7.2±0.7	6.5±0.4	6.3±0.6	6.6±0.5
5	6.7±0.8	6.3±0.7	6.5±0.8	6.5±0.7

[a]Score 1–9, 1 = poor, 9 = excellent.
[b]There were no significant differences ($P > 0.05$) among treatments for any organoleptic property.

Both growth rate (Brett 1979) and thyroid activity (Eales 1979) are elevated in young rainbow trout and, in general, decrease with age (size). Response to dietary goitrogens may be more severe in very young fish, where thyroidal demands may be more acute. In maturing fish, thyroid hormones may modulate gonadotrophic hormone (GTH) secretion (Sage and Bern 1971; Fontaine 1976), as well as influence overall ovarian development (Harvey and Hoar 1979; Lam et al. 1978), and thereby goitrogenesis may be exacerbated by the demands of sexual maturation (Leatherland and Sonstegard 1981). Future studies should include an evaluation of the effects of feeding diets containing canola meal to very young fish or to maturing broodstock to determine the maximum dietary level of canola meal and duration of use for each stage of the life cycle.

In addition, research to determine the mechanism by which dietary glucosinolate hydrolytic products affect thyroid function should continue. Most studies have used TECH, histological appearance of the thyroid, and T_3 and T_4 levels, either singly or in combination, to assess thyroid status. However, histological criteria alone are not adequate indicators of thyroid activity (Yurkowski et al. 1978) and T_3 or T_4 measurements have generally been confined to a single sample taken at the end of an experiment (Yurkowski et al. 1978; this study), which yields a static picture of a dynamic process. Furthermore, information obtained in this manner may be misleading because plasma hormone levels can change fourfold during the course of a day and small differences in sampling time can create significant differences between treatments (Eales et al. 1981; Spieler and Noeske 1979). Future studies should include direct assessment of peripheral (e.g. liver) deiodinase activity and continuous monitoring of plasma T_3 and T_4 levels, as well as histological criteria to assess thyroidal status.

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Predator–Prey Relationships for Juvenile Chinook Salmon, *Oncorhynchus tshawytscha*, Feeding on Zooplankton in "in situ" Enclosures

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ENGLISH, K. K. 1983. Predator–prey relationships for juvenile chinook salmon, *Oncorhynchus tshawytscha*, feeding on zooplankton in "in situ" enclosures. Can. J. Fish. Aquat. Sci. 40: 287–297.

Juvenile chinook salmon, *Oncorhynchus tshawytscha*, were raised in 90-m^3 mesh enclosures in Saanich Inlet, B.C. The enclosures permitted ample water and zooplankton circulation while retaining 5–6 g juvenile salmon. Mean growth rate was 1.8% wet body weight/d over 6 wk. Weekly growth rates ranged from 3.9%/d while food was abundant, to −0.5%/d when food was scarce. Zooplankton concentration inside and outside enclosures without fish were not significantly different. Organisms associated with the sides of the enclosures (non-pelagic) were not a major contributor to the growth of the juvenile chinook. There was a strong relationship between the fish growth rates and the abundance of 1.4- to 4.5-mm zooplankton. Rates of successful search varied directly with the size and inherent contrast of a prey item. The minimum rate of successful search was 2.3 m^3/h for salmon feeding on 1.4- to 4.5-mm zooplankton. This rate of successful search, while far greater than previously suspected, is still within the visual capabilities of the juvenile salmon. The enclosed salmon grew rapidly on zooplankton concentrations that were 1/1000 of those required to sustain similar growth rates in tank experiments.

Key words: predator–prey relationship, planktivorous salmonid, marine, "in situ" enclosures, search efficiency

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Des saumons chinook juvéniles (*Oncorhynchus tshawytscha*) ont été élevés dans des enceintes de filet de 90 m^3 dans l'inlet Saanich (C.-B.). Tout en retenant les saumoneaux de 5–6 g, ces enceintes laissaient circuler librement l'eau et le zooplancton. Le taux de croissance moyen a été de 1,8 % du poids corporel/d pendant une période de 6 sem. Les taux de croissance hebdomadaires ont varié de 3,9 %/d avec abondance à −0,5 %/d avec rareté de nourriture. Les concentrations de zooplancton à l'intérieur et à l'extérieur des enceintes, en l'absence de poissons, ne différaient pas de façon significative. Les organismes associés aux parois des enceintes (non pélagiques) ne contribuèrent pas pour la peine à la croissance des jeunes saumons. Il y avait étroite corrélation entre le taux de croissance des poissons et l'abondance du zooplancton de 1,4–4,5 mm. Le succès de la recherche de la nourriture a varié directement en fonction de la taille et du contraste inhérent des proies. Le taux minimal de recherche réussie a été de 2,3 m^3/h pour des saumoneaux se nourrissant de zooplancton de 1,4–4,5 mm. Ce taux, bien que supérieur à ce que l'on croyait, est quand même dans les limites de capacité visuelle des jeunes saumons. Les sujets élevés en enceintes croissent rapidement à des concentrations zooplanctoniques équivalentes à 1/1 000 de celles requises pour le maintien de taux de croissance identiques dans des expériences en bassins.

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THIS paper describes a relationship for juvenile chinook salmon, *Oncorhynchus tshawytscha*, feeding on natural concentrations of marine zooplankton. Estimates of the predators' search efficiency, a major component of any feeding relationship, are compared to values derived in previous studies.

Many workers have attempted to unravel the critical relationship between juvenile salmon and their pelagic prey.

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Ivlev (1961) concluded that fish feeding was largely dependent on the concentration and distribution of prey. Prey size is another important factor affecting the growth and feeding of juvenile salmon (Lebrasseur 1969; Ware 1972; Wankowski and Thorpe 1979). These and other experiments conducted in tanks suggest that juvenile salmon are inefficient feeders and must feed in dense prey patches to sustain high growth rates (Parsons and Lebrasseur 1970; Beitte and Geen 1980). Tank experiments are strongly biased by two factors: (1) prey concentration in tanks change rapidly as fish feed, and (2) fish densities in tanks have been unnaturally high. Lebrasseur (1969) concluded that further feeding trials, in very large tanks, were necessary because the relationship between food and growth is strongly dependent on the amount of energy expended in searching for and capturing different prey. Warren and Davis (1966), Mann (1966), Paloheimo and Dickie (1966), and Kerr and Martin (1970) all support this conclusion.

To escape the restrictions of tank experiments, this study used large net enclosures where fish growth, survival, and behavior were monitored in relation to natural zooplankton concentrations that changed as natural water masses moved through the enclosures. The study was performed in Saanich Inlet, B.C., a natural feeding area for juvenile salmon.

General Methods

On May 19, 1980, 220 individually cold-branded, juvenile, chinook salmon were introduced into two of four offshore enclosures. An additional 30 branded fish were retained in a laboratory holding tank. The laboratory fish were starved while the fish in the offshore pens could feed on natural zooplankton that moved through their enclosure. The mean initial wet weight of each fish group was 6.2 g, with a mean fork length of 86 mm.

Zooplankton concentrations inside and outside each enclosure were sampled on a day–night basis every 12 h using a vertically hauled 202-μm mesh bongo net. Replicate samples were used to examine the variability between hauls and successive zooplankton counts. The two most recent sets of samples were analyzed each day. Samples were split using a Folsom plankton splitter to maximize counting precision. Zooplankton counts were recorded for four size groups: small (0.7–1.4 mm), medium (1.4–3.0 mm), large (3.0–4.5 mm), and extra large (>4.5 mm). All zooplankton greater than 4.5 mm in body length, medusae, and ctenophores were removed prior to measuring the wet weight of the counted sample. Growth rates for the juvenile salmon were estimated from weekly length and weight measurements for 40 fish from each enclosure. One out of every four fish sampled was killed and immediately preserved for stomach content analysis. Length and weight data were recorded each week for all live fish in the holding tank.

The experimental apparatus consisted of four major components: (1) the flotation platform; (2) the fine mesh net enclosures; (3) a large coarse mesh protection net; and (4) a laboratory holding tank.

The flotation platform (10 m in diameter and 1 m high) was one of three constructed for Controlled Ecosystem Pollution Experimental (CEPEX) projects. Menzel and Chase (1977) describe the flotation module originally used for full-size Controlled Ecosystem Experiments. The structure was permanently moored in 60 m of water in Saanich Inlet.

The enclosures were designed to retain 5–6 g fish while permitting free movement of specific size ranges of zooplankton. Three mesh sizes (1, 9, and 19 mm) were selected to limit the food size available to the fish in each enclosure. The 1-mm mesh enclosure was constructed with black permascreening (flexible window screening). The 9-mm mesh enclosure and the two 19-mm mesh enclosures were constructed with green knotless nylon mesh.

For the purposes of this experiment the four enclosures were placed inside one of the CEPEX flotation platforms. Three rings, constructed of 38-mm polypipe, supported the roughly cylindrical shape of the nets (Fig. 1). The bottom of each enclosure was circular and roughly flat. The sides of the enclosures extended 0.5 m above the water surface to retain jumping fish. The deployment of these enclosures and the methods used to remove phytoplankton fouling are described in English (1981).

The protective net (constructed of 110-mm seine mesh, 10 m in diameter, 17 m deep) was used to prevent predators (primarily dog fish sharks) from damaging the fine mesh enclosures or devouring the juvenile salmon. This net was suspended from the flotation platform and 16 weighted ropes held its sides away from the four enclosures hanging inside.

The holding tank contained 300 L of filtered seawater that was recycled at a constant rate and supplied with adequate oxygen from three air stones. A cooling system, in an adjacent tank, maintained the water temperature at 12 ± 1°C, (similar temperatures to those in the offshore enclosures).

Analytical Methods

Salmon Energetics Model

The energy available for growth is what remains of the food energy ingested after catabolism. The following equation was used to estimate the amount of food consumed (F) in calories.

$$(1) \quad G = F - F \cdot E_r - M_b - M_f(F) - M_s(F)$$

where G is the mean weekly growth rate, and E_r is the portion of food energy loss through excretion. Basal metabolism M_b, feeding metabolism M_f, and swimming metabolism M_s were estimated using equations derived from laboratory experiments by Brett (1964, 1965, 1976).

The amount of food consumed (F) could not be calculated by summing the amounts used for growth and metabolism because both feeding and swimming metabolism are proportional to ration size. Instead, a computer model adjusted the daily caloric intake until the simulated daily growth rates equalled measured mean growth rates. The resulting six values represent the minimum number of calories which the fish must have consumed during an average day in each of the 6 wk they were held in the offshore enclosures.

Losses through excretion account for 25% of total energy intake. This value takes into account both feces and nitrogenous wastes and would apply for most combinations of temperature and ration (Brett and Groves 1979). Elliot (1976)

found significant effects of temperature and body weight on fecal energy loss. However, the ranges of temperature and body weight found in this experiment were not sufficient to necessitate these adjustments. Temperature effects were not included in any of the equations for the following reason. A model including temperature effects on metabolism was compared with the model described in this section. The output of the two models differed by less than 5%. This was expected because metabolic expenditures change very little between 10 and 15°C and the water column temperatures were always within this range.

Brett (1965) describes several equations relating standard metabolism to fish size and temperature. Because temperature effects are minor, the following equation was used to calculate standard metabolism:

$$(2) \quad \text{Log}(M_b) = -0.63 + 0.78 \cdot \text{Log}(W)$$

where W is the wet weight of the fish in grams, and the units for standard metabolism M_b are milligrams of oxygen per hour.

Brett (1976) described the following equation for feeding metabolism M_f in terms of ration size:

$$(3) \quad M_f = (92 + 36.6 \cdot R) - M_b$$

where R is the dry weight of the food consumed as a percent of the fish's dry body weight. The units for feeding metabolism are milligrams of oxygen per kilogram of fish per hour.

The following equation was used to calculate the maximum ration which could be consumed by a fish, depending on its size (Brett 1971).

$$(4) \quad R_{\max} = 14.5 - 5.15 \cdot \text{Log}(W)$$

where W is the fish's wet weight in grams and $R_{\max}$ has the same units as R.

Swimming metabolism or routine activity metabolism can be calculated if one knows the average daily swimming speed of the fish (Brett 1964).

$$(5) \quad \text{Log}(M_s) = 1.85 + 0.27 \cdot V - \text{Log}(M_b)$$

where V is measured in fish body lengths per second and swimming metabolism M_s has the same units as feeding metabolism.

An estimate of the minimum average daily swimming speed was used because the primary function of the model was to provide an estimate of the minimum number of calories consumed by the juvenile fish. Higher swimming speeds would require more food and suggest even higher search efficiencies to support the same growth rate.

The minimum average daily swimming speed is divided into two components: (1) swimming associated with stress or nonfeeding activity and (2) swimming associated with feeding.

An estimate of the nonfeeding activity was obtained from the negative growth rates of the starved fish; in the model, starved fish with an average swimming speed of 1 body length per second lose weight at a rate of −0.9%/d. This model assumes that energy expended in stress or nonfeeding activity would be greatest for a starved fish and least for fish that achieve their maximum ration.

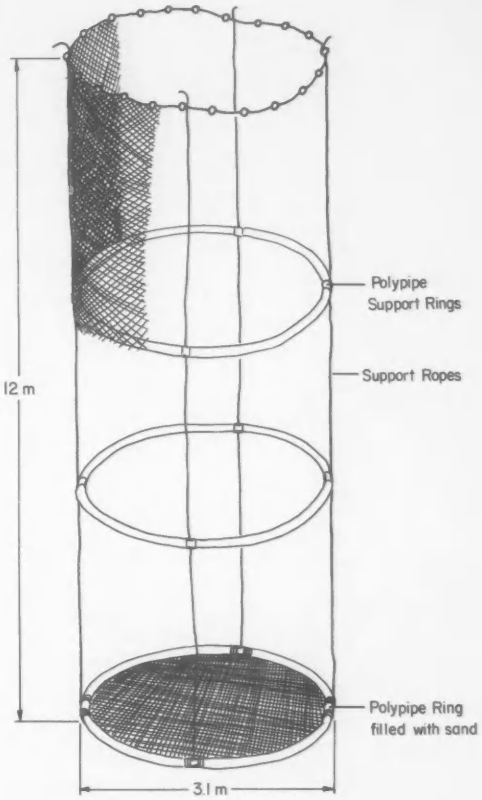

FIG. 1. The fine mesh enclosure.

Hyatt (1978) found that rainbow trout (*Salmo gairdneri*) and sockeye salmon (*Oncorhynchus nerka*) search at speeds of 1−2 body lengths per second when foraging for zooplankton in the water column. Ware (1975, 1978) suggests that the optimal foraging speed for pelagic feeding fish is about 1 body length per second. Therefore, 1 body length per second is a reasonable estimate of the minimum average swimming speed associated with feeding. The following equation describes a conservative relationship between swimming speed and ration size:

$$(6) \quad V = C - (R/R_{\max})$$

where C is 1.5 body lengths per second and R and $R_{\max}$ are as described above. This relationship is consistent with the design of the model (to estimate the minimum number of calories which must have been consumed by the fish).

The above model, crudely translated, is equivalent to gross growth efficiencies of ~19% for small rations and 37% for

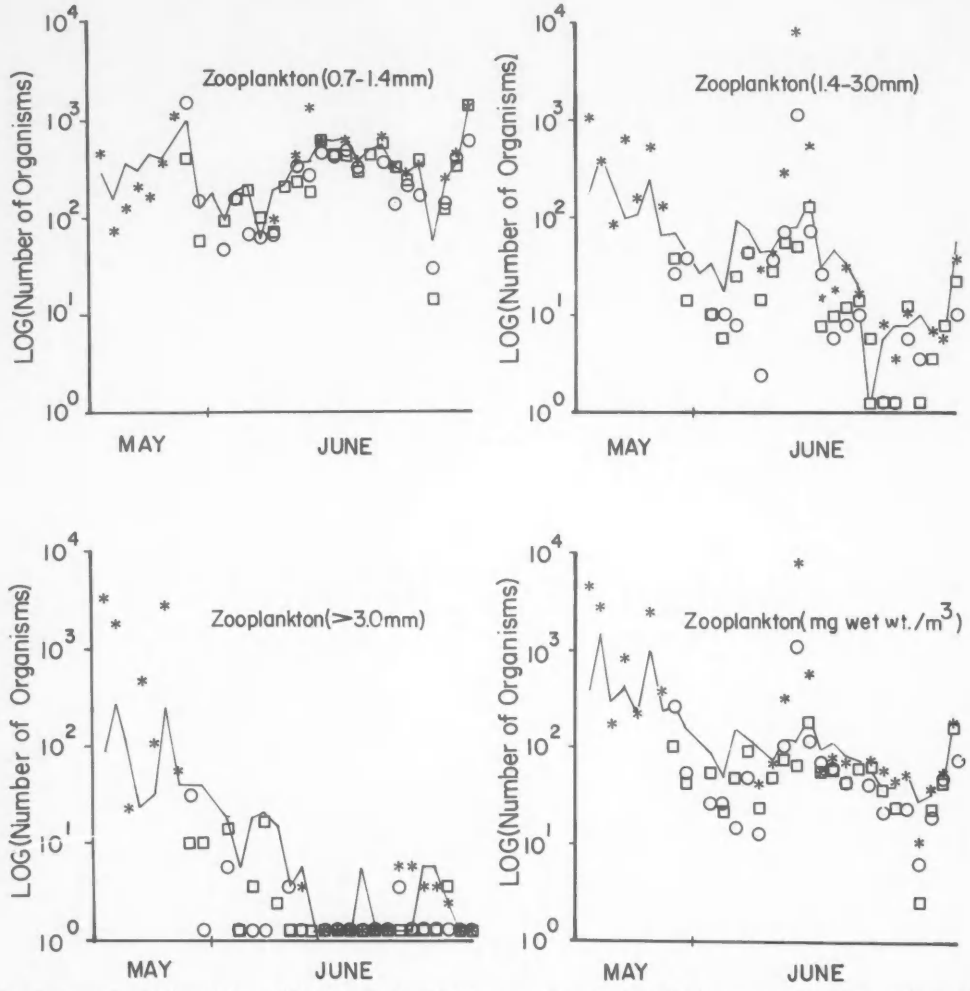

FIG. 2. Spatial and daily variations of "AM" zooplankton abundance per cubic metre. The solid line represents data from samples obtained outside the enclosures (circles: 9-mm enclosure with fish; squares: 19-mm enclosure with fish; asterisk: 19-mm enclosure without fish).

large rations. Biette and Geen (1980) estimate the maximum gross growth efficiency of food conversion in underyearling sockeye salmon to be 18 and 30% for small and large rations, respectively. Therefore, the model probably calculates the minimum amount of food energy necessary to sustain a given growth rate.

MULTISPECIES DISC EQUATION

A multispecies disc equation and several nonlinear function optimization routines were used to calculate relative rates of successful search for nine prey groups. The following formula represents one form of the multispecies disc equation derived by Murdock and Oates (1975):

$$(7) \quad E(n_i) = \frac{\alpha_i \cdot T \cdot n_i}{1 + \sum_i \alpha_i \cdot \beta_i \cdot n_i}$$

where $E(n_i)$ is the amount eaten of the ith prey by each predator, and n_i is the density of the ith prey category in the water column. The parameters in the above equation are T, the total time the predator and prey are exposed to each other each day; β_i, the time spent, by the predator, handling each prey item; and α_i, the predator's rate of successful search.

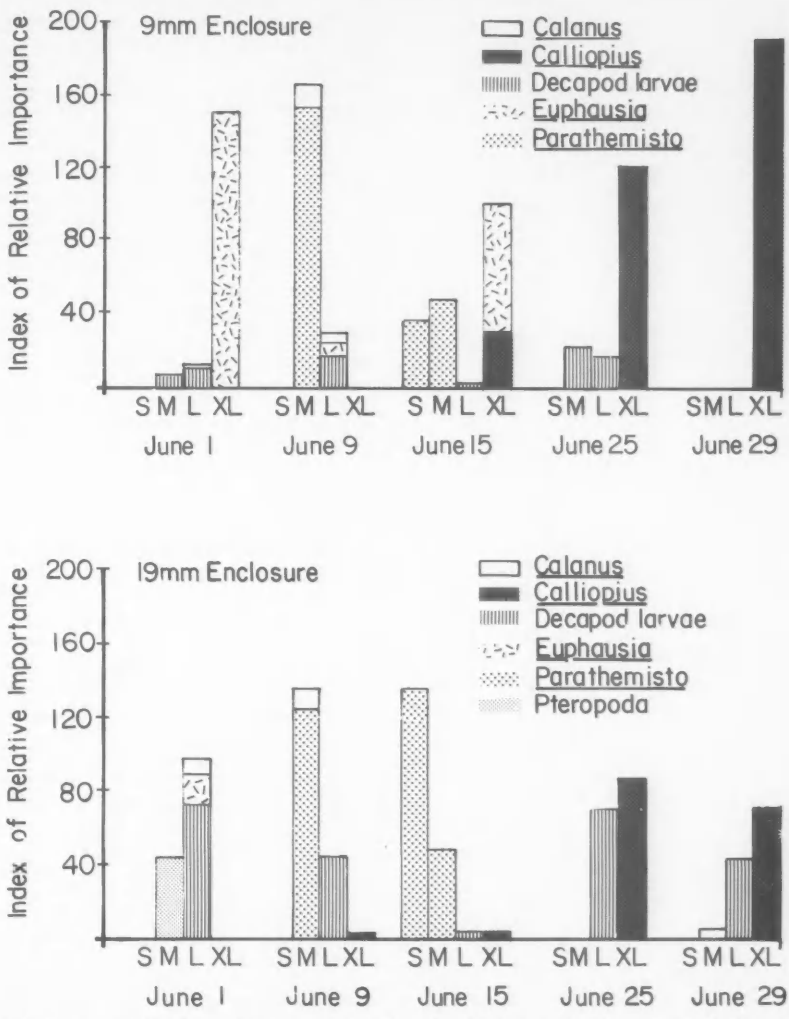

FIG. 3. The relative importance (IRI) of the various types and sizes of prey found in the stomachs of the enclosed fish (S: small; M: medium; L: large; XL: extra large).

The amount eaten $E(n_i)$ during an entire day was extrapolated from stomach content data using the following equation:

$$(8) \quad E(n_i) = \frac{T}{T_d} \cdot S_i$$

where S_i is the mean number of the ith prey found in the stomach contents of 10 fish, T_d is the number of daylight hours before the fish were sampled, and T is as described above. The primary purpose for the above relation was to standardize the stomach content data for the time when the fish were sampled. The relation assumes that food eaten longer than 17 h before the fish were sampled would not contribute to the distinguishable stomach contents. Brett and Higgs (1970) found that juvenile sockeye salmon held in 10 and 15°C water require 19 and 11 h, respectively, to achieve 90% digestion of their stomach contents. Nonetheless, the above relation assumes that the enclosed salmon fed at a constant rate during the daylight hours. Therefore, this relation would overestimate the amount eaten by fish that consume less food during each additional daylight hour. This feeding pattern would be expected for fish that achieve their maximum ration. However, the average fish stomach was less than half full and the number of daylight hours before the

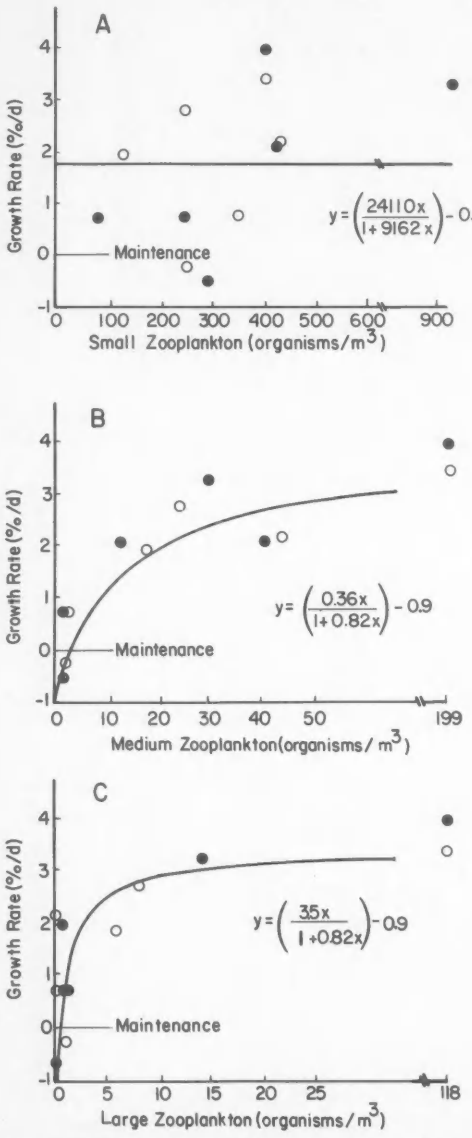

FIG. 4. Relationship between fish growth rates and the abundance of various size-classes of zooplankton prey. The origin represents the growth rate of the starved fish. The curves and equations describe the least squares fit for each data set. Data points represent mean weekly values (closed circles: 9-mm enclosure; open circles: 19-mm enclosure).

fish were sampled was always between 6 and 12 h. Parker and Vanstone (1966) showed that young salmon had a diurnal cycle of feeding intensity and that feeding was continuous during daylight hours. Under these conditions, the above relation would provide a reasonable estimate of the amount eaten during an entire day.

The density of each prey item N_i was derived from daily zooplankton samples obtained outside the enclosures. Data from samples obtained inside the enclosures were of little value because they often did not include several of the prey groups found in the stomach contents. It is probable that the fish significantly reduced the number of zooplankton (especially the more visible species) inside their enclosures.

Blaxter (1970) suggested that a light intensity of about 10 lx, corresponding to late dusk, may be used as a general lower threshold for visual feeders. Because salmon are primarily visual predators, the total time the predator and prey are exposed (T) is equal to the interval between early dawn and late dusk — ~17 h in June.

The time spent handling each prey item (β_i) and the rate of successful search (α_i) for each prey group were estimated using nonlinear function optimization techniques (Patterson 1978). The resulting values should be considered as relative rates because the values for amount eaten, $E(n_i)$, estimated from stomach content data, are not good estimates of the absolute number of each prey consumed each day. However, the mean stomach contents for 10 fish probably provide a reasonable indication of the relative numbers of each prey that an average fish would consume that day.

Evaluation of Experimental Enclosure

The 1-mm mesh permascreening was not suitable material for an experimental enclosure as it was easily torn by moderate wave-and-tidal action and rapidly clogged with phytoplankton growth. Permascreening mesh would be more suitable for a smaller enclosure with more structural support (Laurence et al. 1978). The utility of such an enclosure would be limited to areas or periods of low phytoplankton productivity. The 9- and 19-mm mesh enclosures were much more durable and could be maintained relatively free of phytoplankton fouling.

The idea of using different mesh sizes to limit the food sizes available to the juvenile fish proved to be impractical because of (1) clogging of the smallest mesh size, (2) the 9-mm mesh was not small enough to exclude the largest zooplankton (adult *Euphausia*), and (3) the 19-mm mesh did not screen out any size-class of zooplankton commonly found in Saanich Inlet.

The comparison of zooplankton concentrations inside and outside the enclosures was the single most important analysis used to evaluate the performance of experimental enclosures. Figure 2 illustrates the variations in three size categories of zooplankton gathered from more than 113 daylight "AM" samples. Data obtained from the additional 86 night "PM" samples showed even less variation about the line connecting the data from samples taken outside the enclosures.

Two-way univariate and multivariate analyses were used to investigate the spatial and daily differences in zooplankton concentrations. These analyses revealed highly significant differences ($P < 0.01$) between the zooplankton concentrations inside the two enclosures with fish and concentrations outside the enclosures. However, the zooplankton concen-

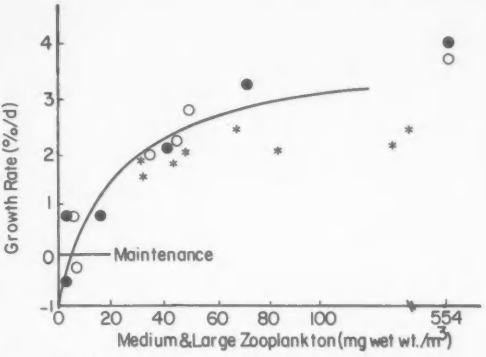

FIG. 5. Relationship between fish growth rates and the abundance of medium and large (1.4–4.5 mm) zooplankters (closed circles: 9-mm enclosure; open circles: 19-mm enclosure; asterisk: data from Johnson 1961).

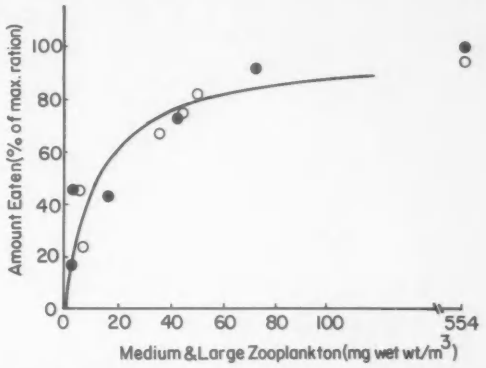

FIG. 6. Relationship between the estimated amount of food eaten and the measured concentration of 1.4- to 4.5-mm zooplankton. Amount eaten is expressed as a percent of the maximum ration to account for changes in mean fish size each week (closed circles: 9-mm enclosure; open circles: 19-mm enclosure).

trations inside the 19-mm mesh enclosure without fish were not significantly different ($P > 0.05$) from those measured outside the enclosures. These results were consistent for each size-class in both "AM" and "PM" samples.

The following suggest that fish, not enclosures, were responsible for the observed differences in the zooplankton concentrations. The concentration of planktivorous predators (juvenile fish) was higher inside than outside the enclosures with fish. The zooplankton concentrations measured inside the enclosures with fish were consistently lower than the zooplankton concentrations measured outside the enclosures or inside the enclosures without fish (Fig. 2).

General Results

The average growth rates of the enclosed fish ranged from 3.9% wet weight/d while food was abundant, to −0.5%/d when food was scarce. The highest individual growth rates in these enclosures (4.9%/d) are very close to the maximum growth rates for similar size of salmon raised on excess rations in the laboratory. Phillips and Barraclough (1978) calculated similar growth rates (4.0%/d) for all species of juvenile salmon residing in Saanich Inlet from the end of May through the middle of June. The salmon held in the laboratory tank without food declined in weight at a rate of 0.9%/d.

The survival rates for the fish in each enclosure were above 90% for the 6-wk experimental period. At the end of the experiment, 106 of the 110 fish initially stocked in the 9-mm enclosure, and 97 of the 110 fish in the 19-mm enclosure, had been recovered alive.

The stomach contents were examined for two reasons: (1) to determine if different prey were consumed by the fish in each enclosure, and (2) to estimate the relative contribution of non-pelagic food items (food items associated with the sides of the enclosures) to the growth of the juvenile fish.

Two-way analyses of variance were used to test for differences in the prey present in the stomach contents between the two enclosures containing fish and among the 5 wk of the experiment. The stomach contents of the fish from the two enclosures were significantly different ($P < 0.05$) in only one of nine prey categories — adult *Euphausia* greater than 15 mm in length were significantly more common ($P < 0.01$) in the stomach contents of the fish from the 9-mm mesh enclosure.

Non-pelagic food sources were not a major contributor to the growth of the juvenile chinook in either enclosure. Nine of the 10 prey groups found in the juvenile chinooks' stomachs could safely be considered pelagic in origin (i.e. not commonly found attached to any substrate). Amphipods, primarily the genus *Calliopius*, were designated the only non-pelagic group. These organisms were seldom captured in zooplankton samples but were consistently observed on the sides of the enclosures.

The relative importance of the various prey groups found in the stomachs was ranked by means of an index of relative importance (IRI). This index reflects the sum of the frequency and volume percentages, multiplied by the percent occurrence value (Pinkas et al. 1971). Figure 3 shows the high relative importance of *Calliopius* in the diet of the juvenile fish during the last 2 wk and the relative insignificance of these organisms during the previous 3 wk. The following observations form the basis for assessing the relative unimportance of non-pelagic food items to the growth of the enclosed fish.

1) The concentration of amphipods on the mesh steadily increased during the experimental period whereas the growth rates of the fish steadily decreased.

2) Growth rates were lowest in both enclosures when amphipods were the most important component of the fish stomach contents.

3) Very few alternative prey were present in fish stomachs during the last 2 wk.

4) Fish were never observed feeding on organisms attached to the sides of the enclosures.

Several other workers have found that juvenile chinook salmon select prey drifting, floating, or swimming in the water column over prey adhering to substrate (Engstrom-Heg 1968; Becker 1973; Higley and Bond 1973).

TABLE 1. Relative rates of successful search by juvenile salmon for the various pelagic prey found in the enclosures.

Calanus			*Parathemisto*		Decapods			*Euphausia*	
S	M	L	S	M	S	M	L	L	XL
0.0	0.02	0.23	1.50	10.0	0.0	0.11	0.34	0.31	2.55
Low contrast			High contrast						

Stomach contents data suggested that small zooplankters 0.7−1.4 mm in body length were seldom consumed by the enclosed juvenile chinook salmon (Fig. 3). Engstrom-Heg (1968) and Craddock et al. (1976) also found that naturally feeding juvenile chinook salmon prefer food items larger than 1.4 mm.

Fish Growth vs. Zooplankton Abundance

Fish growth rates do not appear to be related to the abundance of small zooplankton ($P > 0.5$); however, there appear to be significant relationships between growth and the abundance of larger zooplankters (Fig. 4). This is especially evident if the medium and large size classes are combined ($P < 0.001$, Fig. 5). This figure shows that juvenile chinook salmon sustained maximal growth rates when the concentration of medium and large zooplankton (1.4−4.5 mm in body length) is greater than ~75 mg wet wt/m^3. Below this level growth rates decline very rapidly with each decrease in the prey concentration.

Feeding Response for Planktivorous Salmon

A feeding response curve describes the relationship between the food consumed by a predator and the concentration of the prey. The minimum amount of food the juvenile salmon must have consumed to sustain the observed daily growth rates was calculated from equation (1) and plotted against mean prey abundance for each week (Fig. 6). The curve in Fig. 6 represents the least squares fit of the data to the following Holling single species disc equation.

$$(9) \quad E(n) = \frac{\alpha \cdot T \cdot n}{1 + \alpha \cdot \beta \cdot n} \qquad \begin{matrix} T = 17.0 \text{ h} \\ \alpha = 0.485 \\ \beta = 0.173 \end{matrix}$$

where all the symbols are similar to those described earlier for equation (7). The biological significance of the above parameters can be examined by converting the y-axis units from percent of maximum ration to milligrams wet weight (1% ≃ 9.4 mg wet weight for 100-mm chinook salmon). The predator's rate of successful search is 4.6 m^3/h ($9.4 \cdot \alpha$) and the time spent by the predator handling each prey item is 0.018 h ($\beta/9.4$). If the actual zooplankton concentrations were twice those measured (limit of sampling error), the rate of successful search would be 2.3 m^3/h for this general prey category. Previous tank experiments by Parsons and Lebrasseur (1970) and Lebrasseur (1969) suggested that the rate of successful search is only 0.04 m^3/h for juvenile salmon. Some of the reasons for this major discrepancy are examined in the Discussion.

Relative Rates of Successful Search

Rates of successful search define a predator's capacity to find and capture prey where the density of that prey is low. Relative rates of successful search distinguish the prey that were most readily captured by the predator from those that were captured less frequently.

The relative rates of successful search varied directly with the size and inherent contrast of the prey item (Table 1). The fish searched more effectively for the larger food item within each prey group. Within each size category, higher search rates were calculated for higher contrast prey. The large dark eyes and opaque bodies of *Euphausia*, decapod larvae, and *Parathemisto pacificus* are much higher contrast objects than the transparent bodies common to *Calanus* species. The rates of successful search calculated for *Calanus* species were the lowest in each size category.

Physical Search Capabilities

The results of this study are supported by the physical search capabilities of juvenile salmon. The volume of water a fish could search per unit time (search rate) depends upon swimming speed and reactive distance to potential prey (Hyatt 1979).

Juvenile salmon are primarily pelagic predators that depend upon sight to locate food items. Protasov (1970) proposed that a salmonid's vision is divided into two visual fields: the forward field is used to locate potential food items whereas the backward field warns the fish of an approaching enemy. Protasov's diagrams depict the forward visual field as roughly the shape of a right-angle cone, where the maximum visual area (A) is related to the distance of visibility (d) in the following manner:

$$(10) \quad A = 1.57 \cdot d^2.$$

The area of vision for a feeding fish depends upon the reactive distance of the fish. Many studies have established that the reactive distance is greatly affected by the clarity of the water, the amount of light, and the size and contrast of the prey. Ware (1973) measured the reactive distances of rainbow trout to low contrast targets of various sizes. The following equation describes the curve fitted to Ware's data:

$$(11) \quad d_r = 0.1634 \cdot P^{0.44}$$

where d_r is the reactive distance in metres and P is the prey size in millimetres. Data found in Hyatt (1978), Protasov (1970), and Confer and Blades (1975) suggest similar reactive

distances for fish attacking a variety of natural prey. In all of these studies reactive distances were measured in clear water with ideal illumination. The reactive distances for fish feeding in the enclosures, as in most natural waters, would be greatly reduced due to phytoplankton blooms and suboptimal illumination. Ware (1973) suggests that reactive distance would be decreased by half if the attenuation coefficient were doubled. Measured values of the attenuation coefficients for the euphotic zone are often 2−3 times those of clear laboratory water.

The following equation could be used to estimate the average search rate for juvenile salmon feeding in natural waters:

$$(12)\quad SR = 56.52V\cdot(0.1634Ra)^2\cdot P^{0.88}$$

where SR is the rate of search in m^3/h; V is the predator's swimming speed in cm/s; P is the prey size in millimetres; and Ra is the attenuation of light in natural water relative to that in clear water.

The optimal foraging speed for pelagic feeding fish of about 1 body length per second (Ware 1975, 1978) was used to calculate search rates for the range of prey sizes found in the enclosures (Table 2). The apparent visual capabilities suggest that 2.3 m^3/h is a reasonable estimate for the minimum rate of successful search for juvenile salmon feeding on 1.4- to 4.5-mm prey.

Prey Distribution

Prey patchiness is one of the major factors that may cause temporal variation in the rate of successful search. If prey inside the enclosures were clumped into highly concentrated patches, the fish may have been feeding on much higher concentrations of prey than those estimated from the zooplankton samples. Such a distribution would result in an overestimation of the rate of successful search if the fish obtain a significant portion of their ration in a prey patch. However, the rate of successful search is determined by the initial slope of the functional response when both ration and prey numbers in the enclosures were lowest. If these few prey were highly concentrated, the fish would still have to find these patches and successfully pursue the prey. Under these conditions, the salmon may need an even higher rate of successful search to capture the prey before the patch disperses or moves out of the enclosure.

One might expect that fish, with these relatively high rates of successful search, could significantly reduce the concentrations of food inside the enclosures. This apparently occurred because the concentrations of medium and large zooplankton inside the enclosures with fish were usually about 45 and 65% of the concentrations measured outside these enclosures for day and night samples, respectively. On the other hand, the concentrations of medium and large zooplankton inside the enclosures without fish, and the concentrations of small zooplankton in each enclosure, were frequently greater than 80% of those measured outside.

Discussion

Few workers can be confident that their results concerning the relationship between prey abundance and the food consumed by a highly mobile predator accurately represent the predator's feeding response in its natural environment. To establish this relationship one must be certain that prey concentrations were measured where predators were feeding. This is one of the chief advantages of the methods used in this study. Data from the enclosures suggest that juvenile salmon consumed mostly large, high contrast prey, even when small, low contrast prey are more abundant. Ware (1973) found that prey activity and prey exposure accounted for more of the variation in the diet of a visual predator than did prey density or prey size. Both prey activity and prey exposure are elements which affect the inherent contrast of the prey. The body-size predation hypothesis of Brooks and Dobson (1965) and more recent observations of Zaret (1972) support the importance of prey size and inherent contrast. Zaret suggests that the size of prey *Cladocera* is a less-important cue to planktophages, which hunt visually, than the contrast coloration associated with the eye or digestive tract of the prey species. The importance of these types of visual contrast cues was supported in this study by the relatively high rates of successful search for all prey organisms with large dark eyes.

This paper has examined aspects of fish feeding that lie outside the bounds of conventional tank experiments and most 'in situ' studies. Lebrasseur (1969) found no significant difference between the type or size of prey and the rate of growth sustained by juvenile chum salmon. Lebrasseur suspected that tank experiments reduce the effort required for capturing prey and thereby mask any relationships between prey size and fish growth. Figure 4 confirms his suspicions that larger enclosures and lower prey concentrations would reveal these relationships.

Ivlev (1961), Parsons and Lebrasseur (1970), and others have found that high prey concentrations, which are infrequently measured in nature, are necessary to sustain positive growth rates in tank-raised fish. They contend that these prey concentrations are representative of the patchiness of prey in the natural environment. According to their theory, a fish would have to maintain its position with respect to high concentrations of prey to sustain a high growth rate. The growth rates of the enclosed fish demonstrate that it is not necessary for pelagic-feeding juvenile salmon to follow prey patches. These juvenile salmon were able to sustain high growth rates while feeding opportunistically in a constantly changing water column. The low rates of successful search (0.04 m^3/h) sug-

TABLE 2. Search rates for the range of prey sizes found in the enclosures. The maximum search rates were derived from laboratory measurements (Ware 1973). The probable range assumes that the reactive distances for fish feeding in the euphotic zone is 0.3−0.5 of the laboratory value.

	Rate of search (m^3/h)	
Prey size (mm)	Maximum	Probable range
0.7	11	1.2−2.7
1.5	22	2.4−5.4
3.0	40	4.4−9.9
4.5	57	6.3−14.2
10.0	115	12.7−28.7
20.0	211	23.4−52.8

gested in tank experiments were confounded by two factors: (1) the amount of prey a predator can consume is limited to the amount of prey put in the tank, and (2) concentrations of prey decrease as the predator feeds. None of these tank experiments have removed the effect of prey exploitation or used sufficiently low prey concentration to describe accurately the initial slope of feeding response of a fish.

Laboratory and field work by D. M. Ware and W. E. Johnson provide support for the feeding response described in this study. Ware (1972) estimated that for rainbow trout recognition success (for moving prey) was 74 ± 15% and prey capture success was at least 84 ± 16%. The product of these two factors multiplied by the search rate equals the rate of successful search. Data from Ware (1973) were used to estimate search rates of 4.4–9.9 m^3/h for juvenile salmon feeding on 3.0-mm prey in the euphotic zone (Table 2). These values suggest that the appropriate minimum rate of successful search would be 2.7 m^3/h (0.74·0.84·4.4 m^3/h).

Data presented in Johnson (1961) describe a relationship between the growth of juvenile sockeye salmon and the abundance of zooplankton in Babine and Nilkitkwa Lakes where sockeye weighing 0.2 g in mid-June grow to between 1.2 and 5.7 g by mid-October (122 d), depending on the abundance of zooplankton. Johnson's points representing the lower growth rates for salmon in the lakes are very close to the curve fitted to the enclosure data (Fig. 5). Unfortunately, Johnson's data did not include observations for very low concentrations of zooplankton.

Few workers have attempted to estimate a predator's rate of successful search because this component of a feeding response is probably a complex function of the size, mobility, and camouflage of prey. I did not attempt to estimate absolute values of rate of successful search for each prey species; rather, I propose a minimum value for this factor for a specific size-class of prey organisms. These results suggest that juvenile salmon are far more efficient pelagic predators than was previously suspected.

Acknowledgments

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Influence of Sediment on Anthracene Uptake, Depuration, and Biotransformation by the Amphipod *Hyalella azteca*[1]

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Uptake, depuration, and biotransformation rates of anthracene were determined for *Hyalella azteca* (Amphipoda, Crustacea) in both the presence and the absence of sediment. The mean rate constant ± SE for uptake from water was the same for cases with or without sediment, 255 ± 76 mL·(g animal wet weight)$^{-1}$·h^{-1}. The rate constant for uptake of sediment-associated anthracene was 19 ± 5 g dry sediment·(g animal wet weight)$^{-1}$·h^{-1} for an organic sediment. Depuration increased by a factor of three in the presence of sediment. Sediment-associated anthracene, compound sorbed to sediment and in pore water, was estimated to contribute 77% of the steady-state body burden. These animals, and presumably other benthic organisms exposed to toxicants in organic sediments, are at higher risk than animals not associated with sediments. Further, bioconcentration factors based on the ratio of body burden to water concentration are overestimates for *H. azteca* and other benthic organisms that obtain a large proportion of their body burden from sediment.

Key words: anthracene, *Hyalella azteca*, sediment, PAH

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Les taux d'absorption, de dépuration et de biotransformation de l'anthracène ont été déterminés chez *Hyalella azteca* (Amphipoda, Crustacea) à la fois en présence et en l'absence de sédiment. La constante de taux d'absorption à même l'eau est identique, qu'il y ait ou non sédiment (255 ± 76 mL·(g, poids humide de l'animal)$^{-1}$·h^{-1}; $\bar{x}$ ± ET). Pour ce qui est de l'absorption d'anthracène associé au sédiment, la constante est de 19 ± 5 g de sédiment sec·(g, poids humide de l'animal)$^{-1}$·h^{-1} avec un sédiment organique. En présence de sédiment, la dépuration augmente d'un facteur de 3. On estime que l'anthracène associé au sédiment, composé sorbé au sédiment et dans l'eau interstitielle, contribue 77 % de la charge corporelle en état d'équilibre. Ces animaux et probablement les autres organismes exposés aux toxiques dans des sédiments organiques courent un plus grand risque que ceux qui ne sont pas associés à des sédiments. En outre, les facteurs de bioconcentration fondés sur le rapport charge corporelle:concentration dans l'eau sont surestimés dans le cas de *H. azteca* et autres organismes benthiques qui retirent du sédiment une forte proportion de leur charge corporelle.

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POLYCYCLIC aromatic hydrocarbons (PAH) are ubiquitous, often carcinogenic, pollutants resulting primarily from combustion of fossil fuels. Inputs to aquatic environments are anthropogenic (Hites et al. 1977), as well as natural (Brown and Starnes 1978). Anthropogenic input is projected to increase as energy sources are switched from oil to coal and synthetic fuels (Gehrs et al. 1976). Of primary concern is the bioconcentration of PAH in aquatic biota as a potential vector to man (Neff 1979). The accumulation of these compounds in the aquatic environment also may alter the ecological balance. PAH are associated with tumors in fish and other aquatic organisms (Hodgins et al. 1977; Yevich and Barzez 1977; Bauman 1981) and are acutely toxic to fish and fish larvae at parts per billion levels (Bowling et al. 1983; Hose et al. 1982).

Transfer of toxicants among trophic levels of aquatic food chains has been reviewed by Macek et al. (1979) and Teal (1977), and in only a few cases has toxicant transfer via food been shown to be important (Jarvinen et al. 1977; Weiniger 1978). Because most biomagnification studies have focused

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on fish, the effects of food-source toxicant transfer at lower trophic levels remain unclear. As many benthic organisms ingest sediment and because xenobiotics of major environmental interest are highly sorptive, sediment-associated xenobiotics (i.e. compound directly sorbed to sediments or in sediment pore water) may have major impact on those organisms. Thus, the need to understand the role of sediment-associated xenobiotics on toxicokinetics in benthic organisms is necessary to predict their fate and effects in these organisms.

Here we present rates of anthracene uptake, depuration, and biotransformation by *Hyalella azteca* in both the presence and absence of sediment, with particular emphasis on the role of sediments on the toxicokinetics.

Materials and Methods

Hyalella azteca were dip-netted from ponds at the Botanical Gardens of the University of Michigan, Ann Arbor, MI, and transported to the laboratory in pond water. Animals were held at 24−25°C on a 12:12-h light:dark cycle in shallow aquaria containing algae and macrophytes collected at the same time. Water and sediments for the experiments were collected from Sugarloaf Lake, Washtenaw County, MI. Those sediments contained 5% organic carbon on a dry weight basis (method of Menzel and Vaccaro 1964).

The [9-^{14}C]anthracene (specific activity 1.22×10^8 Bq/mmol, No. 770824, California Bionuclear Corporation) was dissolved in acetone. The radiopurity, determined using thin-layer chromatography (TLC) on silica gel plates (E. Merck, 250-μm coating) with hexane:benzene (4:1 v:v) as solvent, was 99.6 ± 0.04%. All solvents used were of pesticide or HPLC grade. Preparative and analytical procedures were performed under gold fluorescent light ($\lambda \geq 500$ nm) to minimize photodegradation of anthracene.

Filtered (3 μm) Sugarloaf Lake water was labeled in bulk (5 L) and dispensed to replicate test chambers after 1−2 h equilibration. In addition to the experimental pollutant, the water contained acetone carrier solution at no greater than 20 $\mu g \cdot mL^{-1}$. Acetone only marginally affected uptake of nonpolar compounds by fish after 52 d of exposure (Mac and Seelye 1981) and should not have influenced uptake under our experimental conditions. Acetone should not be toxic at these levels as reported toxicity concentration for fish is 6 orders of magnitude higher (Johnson and Finley 1980). Anthracene was presumed to be in solution because all studies were done at, or below, its reported solubility. Actual anthracene water concentrations were determined at each sampling time from measured activity per millilitre and known specific activity. The water concentration was determined to be essentially constant and had a coefficient of variation of 10.5% ($n = 51$) for all experiments.

Uptake rates were determined in quadruplicate in temperature-controlled flow-through chambers containing 0.2 L of water, 30−60 animals, and one of three physical environments: no substratum, sand substratum (washed quartz sand, Mallickrodt Inc.), or Sugarloaf Lake sediment substratum. Labeled water flowing at ~100 $mL \cdot h^{-1}$ maintained constant toxicant-water concentration during the study. The temperature for the studies ranged from 21 to 25°C, with less than 0.5°C variation for each study. Two or three animals were removed at 0.5, 1, 2, 4, and 8 h, weighed, and frozen for later analysis of ^{14}C body burden. *Hyalella azteca* had an average dry to wet weight ratio of 0.27 ± 0.05 ($\bar{x}$ ± SD, $n = 10$).

Depuration rates were determined by transferring the remaining 15−20 labeled animals into flow-through chambers (100 $mL \cdot h^{-1}$) containing unlabeled water for 8 h. Three animals per sample were removed at 0.5, 1, 2, 4, and 8 h after transfer, weighed, and frozen for later analysis.

Animals were analyzed for ^{14}C activity after dissolving in perchloric acid and hydrogen peroxide (Mahin and Lofberg 1966), in a Beckman model LS-150 liquid scintillation counter using 3a70b (Research Products International) scintillation cocktail. The external standards ratio method was used to correct for sample quench after subtracting background.

Biotransformation rates were determined for animals removed after 8 h exposure to anthracene. The animals were kept frozen (−20°C) prior to analysis. Ten to 30 *Hyalella* were extracted twice with 20 mL ethylacetate:acetone (4:1 v:v) and with 20 mL cyclohexane. The extracts were combined and filtered through Whatman No. 1 filter paper, reduced in volume by a combination of rotary flash evaporation and evaporation under a stream of nitrogen to ~500 μL, and analyzed by TLC using hexane:benzene (9:1 v:v) and cyclohexane as solvents. Developed plates were divided into a total of four sections corresponding to anthracene and three other sections, including the origin. The silica gel from each section was scraped from the TLC plate and ^{14}C activity determined. The extracted animal carcasses were also assayed for ^{14}C activity by the same method as the whole animals. Total metabolite was determined as the sum of all non-anthracene ^{14}C on the TLC plate plus unextractable ^{14}C residue.

Water samples (500 mL) removed at the end of the uptake phase of experiments were extracted with three times 100 mL hexane. (The extraction efficiency, based on measurements of ^{14}C activity remaining after extraction, was greater than 99%.) The hexane extracts were combined and dried over anhydrous Na_2SO_4, reduced in volume, and analyzed by TLC as previously described; ^{14}C activity was found to be 97.4% anthracene, indicating that its degradation was negligible in the water after 8 h.

Statistical Analyses

Depuration rate data were fit to a first-order decay model:

$$(1) \quad C_a(t) = C_a(0)\, e^{-K_2 t}$$

where $C_a(0)$ = initial concentration in animal [nmol (g wet wt)$^{-1}$]
K_2 = depuration rate constant (h^{-1})
t = time (h).

Assuming constant uptake and depuration rate constants and water as the only source of toxicant, the concentration of anthracene in the animal (C_a) during the uptake phase of the experiment should be described by the following two-compartment model:

$$(2) \quad \frac{dC_a}{dt} = K_1 C_w - K_2 C_a(t)$$

TABLE 1. Uptake and depuration rate constants for anthracene by *Hyalella azteca*.

Experiment	(Equation 3) Two-compartment model		(Equation 3a)	(Equation 5) Three-compartment model		(Equation 1)
	Water uptake (K_1), mL·(g wet weight)$^{-1}$·h^{-1}	Depuration (K_2), h^{-1}	(K_1), mL·(g wet weight)$^{-1}$·h^{-1}	Water uptake (K_1), mL·(g wet weight)$^{-1}$·h^{-1}	Sediment uptake (K_3), g dry sediment·(g wet weight)$^{-1}$·h^{-1}	Experimental depuration, h^{-1}
No substratum[a]	303±45	0.57±0.7	224±71	—	—	0.22
	212±6	0.15±0.1	193±14	—	—	0.09
	270±48	0.44±0.1	227±54	—	—	0.24
	227±35	0.22±0.07	210±63	—	—	0.06
	432±85	0.52±0.14	311±45	—	—	0.23
	342±85	0.43±0.15	245±19	—	—	0.10
Sand substratum[a]	213±24	0.21±0.43	191±65	—	—	0.12
	250±54	0.38±0.12	215±39	—	—	0.25
Sediment substratum[a]	175±20	0.16±0.04	—	226±16	25±4	0.56
	187±33	0.31±0.88	—	250±42	10±10	0.63
	119±32	0.10±0.09	—	187±37	13±9	0.48
	88±26	−0.03±0.08	—	147±13	27±12	0.23
Average of no-substratum and sand-substratum experiments[b]	218±27	0.37±0.06	227±14	—	—	0.16±0.03
Average sediment substratum[b]	142±23	0.15±0.06	—	202±23	19±5	0.48±0.09

[a]Mean ± SD of estimate from regression.
[b]Mean ± SE of the individual estimates.

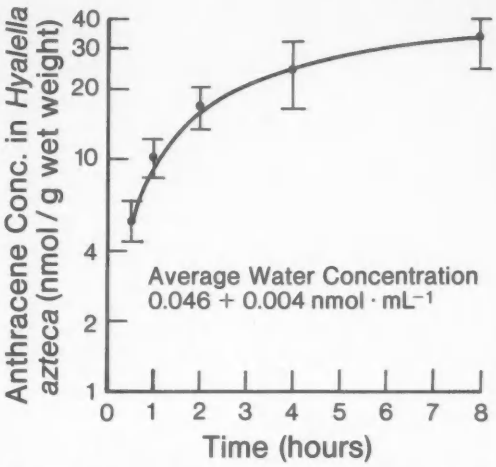

FIG. 1. Uptake of anthracene from water by *Hyalella azteca* in the presence of no substratum and sand substratum. (Points are means ± 1 SD for all experiments, $n = 8$.)

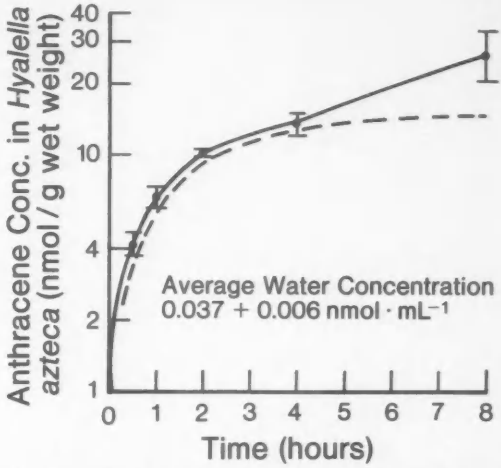

FIG. 2. Uptake of anthracene by *Hyalella azteca* in the presence of Sugarloaf Lake sediment. The theoretical curve represents the contribution of uptake from water only using the rate constants determined from the three-compartment model for uptake from water, the measured depuration rate constants, and measured water concentration. (Points are means ± 1 SD for all experiments, $n = 4$).

where K_1 = uptake rate constant
[mL (g animal wet weight)$^{-1}$·h^{-1}]
K_2 = depuration rate constant (h^{-1})
C_w = water concentration (nmol·mL^{-1})
t = time (h)
C_a = concentration in animals
[nmol (g animal wet weight)$^{-1}$].

It is well to note that most investigators express the uptake rate constants (K_1) in units of h^{-1}. Such units make the assumption that 1 mL of water weighs 1 g and that grams of animal mass cancels grams of water in the kinetic expression. It is more appropriate to express the rate constants as water clearance as that more accurately reflects the process.

If C_w is held constant, as in our experiments, equation (2) has the following solution:

$$(3) \quad C_a(t) = \frac{K_1}{K_2} C_w (1 - e^{-K_2 t}).$$

Time-course measurements of C_a in the absence of sediment or with sand substratum (sand does not adsorb significant amounts of anthracene) were analyzed with this model; K_1 and K_2 were estimated by nonlinear, least-squares regression of C_a on time. Alternatively, K_1 can be estimated using $C_a(t)$ and independently determined K_2 (eq. 1) by averaging:

$$(3a) \quad K_1 = \frac{C_a(t)\, K_2}{C_w(1 - e^{-K_2 t})}$$

for all corresponding $C_a(t)$ and t during each experiment.

Equation (2) is inappropriate for experiments with natural sediment because it does not allow for transfer of toxicants within that compartment. Allowing for the transfer of anthracene from sediment to animal (K_3) and varying the concentration of sediment-associated anthracene, $F(t)$, because the sediment is originally uncontaminated, the following is an appropriate three-compartment model:

$$(4) \quad \frac{dC_a}{dt} = K_1 C_w - K_2 C_a(t) + K_3 F(t).$$

Because equation (4) has no simple solution and because we have independent estimates of K_2 in the presence of natural sediment, time-course measurements of C_a and estimates of $F(t)$ were fit to the following model:

$$(5) \quad \left(\frac{\Delta C_a}{\Delta t} + K_2 C_a(t)\right) = K_1 C_w + K_3 F(t)$$

with linear, least-squares regression. Derivatives ($\Delta C_a / \Delta t$) were estimated directly from data collected at times 0, 0.5, 1, 2, 4, and 8 h. $C_a(t)$ corresponding to each derivative estimate was calculated as the average between measurements; C_w was held constant. Because sediment and pore water were originally without anthracene and because the partition coefficient between water and organic sediment is of the order 10^4 (Karickhoff 1981), one would expect the pore water to achieve a concentration no greater than that of the overlying water, especially in only 8 h. The rate constant for uptake from pore water would thus be indistinguishable from that for overlying water and any increased flux of toxicant to the animal would thus be attributable only to that sorbed to sediment. $F(t)$ was assumed to vary according to the sorption kinetics of anthracene on high organic sediment (Giesy et al. 1982) (organic carbon content 20%; J. Haddock, Savannah River Ecology Laboratory, Aiken, SC, personal communication).

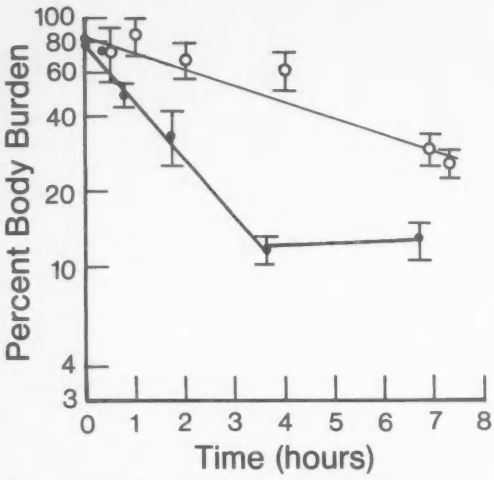

FIG. 3. Elimination of anthracene by *Hyalella azteca* in the presence of no substratum and sand substratum (open circles) and in the presence of Sugarloaf Lake sediment (closed circles). All data were used to determine the regression lines (points plotted are means ± 1 SE). The percent body burden for each experiment was based on the body burden after 8 h of uptake.)

Analyses of equation (3) for experiments with sand or no substratum and of equation (5) for experiments with natural sediment provide independent estimates of uptake constants from water (K_1). Analysis of equation (5) also provides an estimate of uptake kinetics of sediment-associated anthracene (K_3).

Comparison of differences between means of data sets were determined using Students t test.

Results

UPTAKE

Anthracene accumulation rates from water in experiments with no substratum and with sand substratum were the same (Table 1). The water concentrations under the two experimental conditions were the same: 0.046 ± 0.004 nmol·mL^{-1} ($\bar{x}$ ± 1 SD, n = 30 averaged over all sample times and all experiments without a substratum and with sand substratum). Uptake in these experiments followed the two-compartment model and the body burden approached steady state after 8 h (Fig. 1).

Uptake of anthracene in the presence of Sugarloaf Lake sediment was more complex and followed the three-compartment model. Body burden did not approach steady state after 8 h for these animals (Fig. 2). Although anthracene flux to the experimental chambers was the same, sediment sorption caused reduction in water concentration for these experiments (0.036 ± 0.006 nmol·mL^{-1}, $\bar{x}$ ± 1 SD, n = 20 averaged over all time points and experiments employing Sugarloaf Lake sediment as substratum). In spite of lower water concentration and faster depuration rates (see discussion on depuration), the body burden at 8 h was not significantly different than in the studies with no substratum or sand substratum.

Sediment-sorbed anthracene residing in the gut of the animals may not be totally bioavailable but it would contribute to the overall body burden and impact estimates of uptake and biotransformation. We estimate the contribution of the gut contents by two methods. The first method is based on animal ash content and assumes a 5% sediment organic carbon content (same as the bulk sediment). Ash content for amphipods averages 21 ± 7.2% of dry weight (Johnson and Brinkhurst 1981; Salomn et al. 1976) and the dry to wet weight ratio for *H. azteca* is 0.27 ± 0.06. Based on projected sediment anthracene concentrations ($F(t)$ from above) and measured body ^{14}C activity at 8 h, the percent contribution to the overall body burden would be 0.06 ± 0.008 ($\bar{x}$ ± SD for all experiments using Sugarloaf Lake sediment substratum).

Because it may be likely that *H. azteca* would preferentially ingest the organic portion of the sediment, the potential contribution of sediment-sorbed anthracene was also estimated by comparing the time-zero intercepts of the depuration curves. Assuming gut contents are eliminated rapidly before or in conjunction with the first depuration measurement, animals from the sediment experiment should yield a lower time-zero concentration expressed as percent body burden measured after the 8-h uptake experiment. The 5% difference between time-zero estimates for animals in the sediment experiment and the no-substratum and sand-substratum experiments suggests the contribution of gut-anthracene only minimally affects the kinetics and biotransformation estimates.

Rate constants for anthracene uptake from water as determined with the two-compartment model (eq 3) for animals exposed to water only (no substratum) or to water in the presence of a sand substratum are statistically indistinguishable, and are both higher than rates for animals exposed to natural sediment (Table 1). The lower rate in the presence of a natural substratum results from the bias due to violating the assumptions of the two-compartment model. However, rate constants for uptake from water for animals exposed to natural sediment, determined with the three-compartment model, are not statistically different from those determined with other substrates (Table 1). The rate constants for anthracene uptake from water are within the range of values previously determined for other benthic and pelagic invertebrates (Gerould et al. 1983; Landrum 1982; Herbes and Risi 1978).

The rate constant for uptake of sediment-associated anthracene in the presence of natural sediment is 19 ± 5 g dry sediment (g animal wet weight)$^{-1}$·h^{-1}. This estimate is dependent on the values used for $F(t)$ (eq 5), which are based on sorption−desorption kinetics of a sediment of somewhat different composition. Although both were high in organic carbon, the sediment from Sugarloaf Lake was 5% organic, whereas that used for $F(t)$ (Giesy et al. 1982) was 20% organic. Because organic pollutants partition in proportion to the organic content of the sediment (Karickhoff 1981), the amount of anthracene in the 20% organic sediment would be higher than is actually sorbed to our sediment. To maintain the same anthracene flux to our animals, given the assumed (higher) values for $F(t)$, our sediment-associated uptake rate constant estimate would have to be low. As a result, our

TABLE 2. Biotransformation of anthracene by *Hyalella azteca*.

Experiment	Water concn, nmol·mL^{-1}	Body burden at 8 h, nmol·g wet wt	Biotransformation rate at 8 h, nmol·g^{-1} dry wt·h^{-1}	Biotransformation rate constant, h^{-1}	Ratio bound to extractable metabolite
No substratum	0.043–0.049	34±8[a] (n=6)	2.2±0.5[a] (n=6)	0.024±0.005[a] (n=6)	0.72±0.08[a] (n=6)
Sand substratum	0.043	32±11 (n=2)	3.0±0.08 (n=2)	0.030±0.007 (n=2)	0.75±0.13 (n=2)
Sediment substratum	0.043–0.037	35±10 (n=4)	1.0±0.15 (n=4)	0.014±0.005 (n=4)	0.42±0.06 (n=4)
Average for no-substratum and sand-substratum experiments	0.043–0.049	33.5±8 (n=8)	2.4±0.5 (n=8)	0.025±0.005 (n=8)	0.72±0.06 (n=8)

[a] $\bar{x}$ ± SD.

estimate should be considered only of order-of-magnitude accuracy but certainly conservative and demonstrative of the impact of sediment-associated uptake.

DEPURATION

Animals in the presence of natural sediment eliminated ^{14}C-labeled compounds significantly faster ($P < 0.005$) than those in the presence of no substratum or sand substratum (Table 1, Fig. 3). Elimination in the presence of natural substratum appeared to be biphasic and no change in body burden was observed after 8 h. Presence of a substratum other than pure sand has previously been shown to increase the elimination rate of PAH (Gerould et al. 1983; Leversee et al. 1982; Landrum 1982). Depuration rate constants estimated from the two-compartment model (eq 3), however, suggest that depuration is slower in the presence of organic sediments. This disagreement between independently determined depuration constants and those estimated via the two-compartment model has not been observed previously and is attributable to bias introduced by violating the assumptions of the two-compartment model. That is, by ignoring the large contribution of anthracene from sediment, estimated depuration rates have to be artificially lower in the two-compartment model to compensate for the increased body burden.

BIOTRANSFORMATION

Hyalella azteca biotransformed anthracene at a rate of ~2.1% of the body burden per hour at 8 h (Table 2). The rate is much greater than that found for the cold-water amphipod *Pontoporeia hoyi* (Landrum 1982) and much lower than that found for the midge larvae *Chironomus riparius* (Gerould et al. 1983). The biotransformation rate constant at 8 h was determined by dividing the biotransformation rate, based on body residue, by the concentration of the parent compound at 8 h. This constant was significantly smaller ($P < 0.005$) for animals in the presence of natural sediment as compared with animals in the presence of sand substratum or no substratum.

The ratio of non-extractable, "bound" metabolites to extractable metabolites is higher (0.72 ± 0.06) for the no-substratum and sand-substratum experiments than for the natural-sediment experiments (0.42 ± 0.05; $P < 0.01$). Higher fractions of nonextractable metabolite imply greater binding of the metabolite by the organism. Binding of PAH metabolites to macromolecules, in particular DNA and RNA, is the mechanism by which these compounds exert their chronic toxic effects and has been clearly demonstrated for some aquatic species (Varanasi et al. 1981).

BIOCONCENTRATION FACTORS (BCF)

The BCF can be estimated from the ratio of the rate constants for uptake from water and for depuration. The BCF must be estimated from the kinetics in this case because steady state was not achieved in the experiments. BCF based on total ^{14}C will be an overestimate if biotransformation is not accounted for (Leversee et al. 1982). For example, the BCF for the no-substratum and sand-substratum experiments was estimated to be 2089 ± 366 without biotransformation correction. Correcting the total ^{14}C body burden for the fraction of metabolite at 8 h reduces the BCF to 1800 ± 329. The BCF is higher than that found for anthracene with *C. riparius* (132 ± 39; Gerould et al. 1983) and *Daphnia pulex* (760; Herbes and Risi 1978) determined from similar experiments. However, the BCF is much lower than that estimated for the cold-water amphipod *P. hoyi* (16800; Landrum 1982).

BCFs calculated as above are inappropriate for animals in the presence of natural sediment because sediment-associated toxicant contributes to total uptake. For this case, we use the ratio of estimates of steady-state body burden to source concentration. (Note the sediment-sorbed anthracene in the gut was estimated to contribute no more than about 5% as previously discussed.) The former was estimated by steady-state solution of the three-compartment model (eq 4) with parameter estimates from regression (Table 1). The steady-state value of F, 1852 mg·g dry weight^{-1}, was calculated from partition characteristics of high organic sediments (Giesy et al. 1982) and our water concentration. The animal body burden at steady state divided by the water concentration is 10985 ± 2368. When corrected for biotransformation, the BCF estimate becomes 9096 ± 1960. This water-concentration-based BCF estimate is, however, misleading because, in our experiments, the sediment contributes an estimated 77% of the body burden at steady state for *H. azteca*. The bioaccumulation factor calculated from the ratio of the steady-state body

burden (wet weight basis) to the amount of anthracene in the sediment (dry weight basis) was 41 ± 10. If one assumes that anthracene is associated only with the organic portion of the sediment (5% by weight), then the bioaccumulation factor becomes 2.4 ± 0.4.

Discussion

Anthracene uptake by benthic invertebrates can occur via the respiratory surface, the body wall, and the ingested anthracene-laden particles. For *H. azteca*, the first two modes of uptake will occur from contact with both overlying water and pore water. Because uptake from water usually occurs primarily via the respiratory membrane, changes in respiration could affect uptake. Although the presence or absence of a substratum effect changes in benthic invertebrate respiration (Provini and Marchetti 1976; Vernberg and Vernberg 1977), and changes in respiration affect DDT uptake by fish (Murphy and Murphy 1971), we found no differences in rates of uptake, elimination, or biotransformation for animals with or without an inert sand substratum. This indicates that changes in respiration occurring as a result of the absence of a substratum are not sufficiently large to alter the toxicokinetics of anthracene in *H. azteca*.

In the presence of Sugarloaf Lake sediment, initial uptake rates were controlled primarily by uptake from water; however, as the sediment became charged with anthracene, the kinetics were controlled additionally by sediment-associated uptake. In spite of 20−30% lower water concentration due to the loading of the natural sediment, body burden after 8 h was indistinguishable from experiments with no substratum or sand substratum. Further, the animals in the no-substratum and sand-substratum experiments approach steady state after 8 h whereas the animals in the presence of Sugarloaf Lake sediment have steadily increasing body burdens as a result of sediment ingestion. (As described above, pore water contribution would not be distinguishable from that of the overlying water for this experimental design.)

The sediment contribution at steady state was estimated to be 77% of the total body burden. This apparent excessive food-based source is unusual in that it has been observed only for DDT and PCB (Macek et al. 1979; Weiniger 1978; Southworth et al. 1979; Teal 1977; Chadwick and Brocksen 1969; Hansen 1980). More recently, however, J. F. McCarthy (Oakridge National Laboratory, Oak Ridge, TN, personal communication) found a significant contribution of benzo[*a*]pyrene and anthracene via food for *Daphnia* feeding on yeast.

The sediment-associated uptake rate constant is high, 19 ± 5 g dry sediment · g animal wet weight^{-1} · h^{-1}, and even if the anthracene were only in the organic portion of the sediment, the rate constant would imply that the animals process 0.95 ± 0.4 g organic carbon · g animal wet weight^{-1} · h^{-1}. These very high rates suggest that animals are obtaining toxicants other than via ingested sediment or that the PAH is associated even more preferentially within the organic material and it is only that fraction that is being ingested by *Hyalella*. The latter may be likely because amphipods have upper food-size cutoffs of about 30 μm (Ankar 1977) and the finer-grained material should be more highly sorptive, with a large surface area to mass ratio and a high organic content. This has also been suggested (Eadie et al. 1982a) to account for the bioaccumulation of PAH by *P. hoyi* in environmental samples.

Depuration was rapid and followed first-order loss for the experiments with no substratum or sand substratums. In the presence of Sugarloaf Lake sediment depuration was faster and biphasic, the second phase beginning after 4 h with 10−15% of the body burden remaining. This 10−15% of the body burden is likely a slow release compartment existing perhaps as bound metabolite.

The presence of natural sediment not only increased overall rates of uptake (sum of uptake from water and sediment) and elimination (Table 1), but also decreased the apparent biotransformation rate and "binding" of metabolite (Table 2). The lower biotransformation rate results probably from bias due to increased metabolite elimination in the presence of sediment. The rate was calculated as the micrograms of metabolite accumulated in the animal, divided by the duration of the experiment. (The rate constant simply normalizes this rate to the body burden of anthracene at the end of the experiment.) The increased ^{14}C elimination rate is probably due to increased elimination of metabolite because the relative pool size of bound metabolite decreased in the presence of natural sediment (Table 2). Because elimination increased and apparent biotransformation decreased both by factors of 2.5−3.0, it is likely that the biotransformation rate determined in either sand substrate or no substrate is closer to the actual rate. Of course, even these are possibly underestimates due to elimination of metabolite.

Data presented here suggest that BCF, as usually calculated, is an inappropriate comparison for benthic organisms and will result in artificially elevated values because the body burden is achieved by uptake from both water and sediment. Bioaccumulation factors in relation to sediment concentrations may be better measures of the overall magnification of the compound. In fact, our BCF calculated from dry sediment is similar to bioaccumulation factors for PAH in benthic organisms of Lakes Michigan and Erie (Eadie et al. 1982a, b).

While natural sediment appears to increase both total uptake and elimination of anthracene, the net effect is an increased body burden. Extrapolating data from the sediment experiments to steady state indicate body burdens will be increased by a factor of five in the presence of sediment. Although our microcosms are crude simplifications of nature, our data indicate that *H. azteca*, and presumably other benthic organisms, are apparently at greater risk from pollutants that sorb to sediments than are their free-swimming neighbors.

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Biological and Toxicological Effects of Environmental Contaminants in Fish and Their Eggs

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NIIMI, A. J. 1983. Biological and toxicological effects of environmental contaminants in fish and their eggs. Can. J. Fish. Aquat. Sci. 40: 306–312.

Rainbow trout (*Salmo gairdneri*), white sucker (*Catostomus commersoni*), white bass (*Morone chrysops*), smallmouth bass (*Micropterus dolomieui*), and yellow perch (*Perca flavescens*) were collected from Lakes Ontario and Erie to examine the relationship between contaminant levels in females and their eggs. Factors such as the percent lipid in the fish and percent of total lipid deposited in the eggs significantly influenced ($P < 0.01$) contaminant transfer. The percentages of the 9–11 organic contaminants transferred generally showed less variation within a species than the percentages for a substance transferred among the five species examined. This relationship was consistent even though there was over a 10-fold range in contaminant concentrations within a given species. Mercury did not demonstrate this response because the percentage in eggs was low for all species. The levels of PCB monitored in eggs of rainbow trout collected from Lake Ontario suggest that egg and fry survival rates could be affected based on the toxicological evidence from other studies. An examination of the possible effects of spawning on the kinetics of contaminants among these species suggests that relative body concentrations of organic contaminants may be decreased by 5% or be increased by 10%, and mercury levels may be increased by 6–22% following the deposition of eggs. The amount of change varies with species and is influenced by the percent egg weight of body weight, and the rate of contaminant transfer from females to eggs.

Key words: toxicology, contaminants, reproduction, Lake Ontario, Lake Erie

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Des échantillons de truites arc-en-ciel (*Salmo gairdneri*), de meuniers noirs (*Catostomus commersoni*), de bars blancs (*Morone chrysops*), d'achigans à petite bouche (*Micropterus dolomieui*) et de perchaudes (*Perca flavescens*) ont été capturés dans les lacs Ontario et Érié dans le but d'étudier la relation entre les niveaux de contaminants chez les femelles et leurs oeufs. Le transfert de contaminants est nettement influencé ($P < 0{,}01$) par des facteurs tels que le pourcentage de lipides dans le poisson et celui des lipides totaux déposés dans les oeufs. Les pourcentages des 9–11 contaminants organiques transférés montrent généralement moins de variation au sein d'une espèce que ceux d'une substance particulière transférée d'une espèce à l'autre, parmi les cinq espèces étudiées. Cette relation est uniforme, en dépit du fait que, chez une espèce donnée, les concentrations de contaminants couvrent un éventail dont les valeurs supérieures peuvent être dix fois plus grandes que les valeurs inférieures. On n'a pas observé le même phénomène pour le mercure car sa concentration dans les oeufs était faible pour toutes les espèces. Comme l'indiquent les résultats d'autres études toxicologiques, les concentrations de BPC relevées dans les oeufs de truites arc-en-ciel prélevées dans le lac Ontario pourraient influer sur le taux de survie des oeufs et des alevins. Si l'on s'arrête aux effets possibles de la ponte sur la cinétique des contaminants chez ces espèces, on constate que les concentrations de contaminants organiques dans le corps pourraient diminuer de 5% ou augmenter de 10%, alors que les niveaux de mercure pourraient augmenter de 6 à 22% une fois les oeufs déposés. Le degré de changement varie selon l'espèce et est influencé par le poids des oeufs par rapport à celui du corps, et par le taux de transfert des contaminants des femelles à leurs oeufs.

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THE management of a fishery that is viewed as a renewable resource is based on the premise that the species will perpetuate itself. Stock managers have long recognized that factors such as temperature and food supply can influence recruitment, but recent information on environmental quality suggests the presence of toxic substances can affect survival rate. Environmental monitoring and surveillance programs, which commonly use fish as the principal indicator, have reported elevated levels of contaminants in biota from many major water bodies and in some cases note that fish have attained concentrations that are of concern when viewed from a human health perspective (IJC 1980). The toxicological effects of these contaminants on the fish population are largely unknown.

One aspect of the biology of species inhabiting perturbed environments that has received little attention is the relationship between the contaminant levels in spawning fish and that passed to their reproductive products. Some studies have reported reduced survival rates of eggs and larvae containing levels of polychlorinated biphenyls (PCB) in the $mg \cdot kg^{-1}$ range (Johansson 1970; Hogan and Brauhn 1975). Other studies have observed lower survival rates among the progeny of parents that were exposed to mirex (Buckler et al. 1981), and monitored the redistribution of a PCB in the body during gonadal maturation (Guiney et al. 1979). These studies have demonstrated the effects of contaminants on reproductive success, but were limited to observations on a single substance in one species and did not identify the biological factors that influence the transfer of residues from fish to gametes. The present study examined the transfer of 12 environmental contaminants between females and eggs among five species to identify specifically the factors that influence this process. The toxicological implications of the contaminant concentrations monitored in these species and the probable role spawning may have on contaminant dynamics were also reviewed.

Materials and Methods

Nine gravid rainbow trout (*Salmo gairdneri*) and nine white suckers (*Catostomus commersoni*) were captured in mid-April from Lake Ontario during their spawning migration. Trout were taken at the Ganaraska River and suckers at the Humber River. Eight white bass (*Morone chrysops*) and eight smallmouth bass (*Micropterus dolomieui*) were collected prior to spawning in mid-April and late May, respectively, from the western basin, and eight yellow perch (*Perca flavescens*) were collected in late April from the central basin of Lake Erie. All fish were frozen upon capture.

Fish were prepared for analysis according to the following procedure. Residual material in the digestive tract was removed after thawing; then each fish was weighed. Both ovaries were removed, and eggs from the anterior, middle, and posterior sections were blended for analysis. The remaining whole fish was then ground to a uniform composition with a grinder, then a blender. All samples were refrozen until analysis. A muscle sample was taken from each trout for another study but both muscle and whole fish samples were analyzed and the contaminants levels for this species were mathematically adjusted to represent whole fish values.

Analyses for organic contaminants included the following steps. A 10-g fish sample was thoroughly mixed with 25 mL anhydrous sodium sulfate (Na_2SO_4) in a jar and allowed to stand for 30–40 min. The mixture was transferred to a 25 × 595 mm Teflon stoppered chromatographic column with a glass wool plug which contained 5 cm Na_2SO_4 and 75 mL methylene chloride (CH_2Cl_2). The jar was rinsed with 15 mL CH_2Cl_2 which was also added to the column. After standing for 30 min, the CH_2Cl_2 was allowed to drip 6–8 $mL \cdot min^{-1}$ into a 300-mL round-bottomed flask. When the CH_2Cl_2 drained to within 2.5 cm of the sample top, successive volumes of 100 and 55 mL CH_2Cl_2 were added and allowed to drip into the flask. The eluent was collected and the volume was reduced to less than 100 mL using a rotary evaporator. The sample was transferred to a volumetric flask and made up to 100 mL with CH_2Cl_2. A 10-mL aliquot was pipetted into a stoppered graduated centrifuge tube and gently blown to near dryness using a stream of air; then hexane was added to obtain a 1-mL sample.

To separate the residue fractions, Florisil was added to a 6 × 390 mm Teflon stoppered chromatographic column to form a 24-cm bed. The 1-mL sample was immediately applied to the column using a disposable Pasteur pipette and the sample tube was rinsed twice with 0.5 mL hexane which was added to the column. Successive 1.5-mL portions of hexane were added until the entire column was wetted. A glass-jointed reservoir was placed on top of the column and 30 mL of hexane was added and eluted. This fraction contained PCBs, hexachlorobenzene (HCB), mirex, and *p,p'*-DDE. A 15-mL mixture of 25% CH_2Cl_2 in hexane (v/v) was then added and eluted. This fraction contained α, β, and γ lindane, α and γ chlordane, *p,p'*-DDD, and *o,p'*- and *p,p'*-DDT. Fifty millilitres of CH_2Cl_2 was then added to the reservoir and eluted. This fraction contained heptachlor epoxide, dieldrin, oxychlordane, and α and β endosulfan. The three fractions were reduced in volume using a warm water bath and blown to near dryness with air. The samples were prepared for chromatographic analyses by adding 2 mL of 10% benzene in hexane.

The samples were examined by a gas chromatograph equipped with an electron capture detector. The first fraction was analyzed using a 3.7 m × 2 mm glass column packed with 3% Dexil on Chromosorb WHP. Injection, column, and detector temperatures were 300, 240, and 350°C, respectively. The 5% methane:95% argon carrier gas flow was $24 mL \cdot min^{-1}$. The second fraction required a 30 m × 0.3 mm OCl fused silica WCOT column. Injection and detector temperatures were 250 and 350°C. Column temperature was 90–240°C at $4°C \cdot min^{-1}$, 2 min hold-initial, 4 min hold-final. Helium carrier gas flow was 2.5 $mL \cdot min^{-1}$, and 5% methane:95% argon makeup and gas flow was 40 $mL \cdot min^{-1}$. The third fraction required a 3.7 m × 2 mm glass column and detector temperatures were 250, 210, and 300°C. The 5% methane:95% argon carrier gas flow was 22 $mL \cdot min^{-1}$.

Mercury concentrations were determined by atomic absorption using the cold vapour technique. A 0.2-g sample was placed in each test tube containing a mixture of sulfuric and nitric acids and heated to 90°C overnight. The samples were then heated to 220°C (fuming) to facilitate oxidation. After cooling, 1.5 mL of a 6% potassium permanganate solution

TABLE 1. Fish and egg weight and lipid levels among the five species examined. The values shown represent the mean and standard deviation. Regression analyses between the relationships of fish weight on percent lipid and egg weight are also shown for each species. Equations that are statistically significant at the $P \lesssim 0.05$ level are indicated by an asterisk after the F-value.

Parameter	Rainbow trout (n=9)	White sucker (n=9)	White bass (n=8)	Smallmouth bass (n=8)	Yellow perch (n=8)
			Whole fish		
Weight, g	3916±1038	933±227	503±83	969±348	315±144
	2200–5330	608–1338	393–635	509–1423	110–500
Lipid, %	11.4±2.1	6.2±2.1	8.5±1.1	6.2±1.7	5.1±2.0
	8.0–15.6	5.1–7.3	6.8–10.2	3.6–8.9	2.2–7.6
			Fish less eggs		
Weight, g	3382±901	766±178	461±71	895±311	243±110
	1861–4665	504–1070	372–574	484–1312	89–394
Lipid, %	12.2±2.5	6.2±0.9	8.4±1.1	5.6±1.7	4.9±2.2
	8.1–17.2	5.0–7.6	6.8–10.1	3.0–8.4	1.6–8.1
			Eggs		
Weight, g	533±175	166±51	43±13	74±38	72±35
	305–823	104–268	21–61	25–123	21–110
Lipid, %	8.7±0.9	5.7±0.5	9.7±1.2	13.4±1.7	5.8±2.0
	7.2–9.8	4.8–6.4	7.0–11.0	10.4–15.8	4.5–10.5
% Eggs of total weight	13.6±2.5	17.6±1.3	8.4±1.7	7.4±1.6	22.3±3.2
	9.6–17.3	16.1–20.0	5.3–10.7	4.9–9.3	18.2–27.1
% of total lipid in eggs	10.7±3.3	16.4±3.3	9.7±2.3	17.2±5.9	27.1±7.2
	5.7–15.9	11.3–21.1	6.2–13.3	9.6–25.3	15.7–40.6
			Fish weight in g (X) vs. percent lipid (Y)		
Regression analysis					
Equation	Y=9.4+0.000X	Y=8.3−0.002X	Y=6.7+0.004X	Y=4.3+0.002X	Log$Y$=−1.1461+0.625Log$X$
r^2, F-value	0.06, 0.43	0.36, 3.99	0.07, 0.47	0.17, 1.26	0.66, 11.84*
			Fish weight in g (X) vs. % eggs weight (Y)		
Equation	Y=13.8+0.000X	Y=14.0+0.004X	Y=2.1+0.013X	Y=4.3+0.003X	Y=19.2+0.010X
r^2, F-value	0.00, 0.00	0.46, 6.06*	0.40, 3.92	0.50, 6.07*	0.20, 1.46

was added to complete the oxidation. A 30% hydrogen peroxide solution was added dropwise after 2 h to remove the brown precipitate. The samples were then made up to 60 mL. A portion of each sample was then transferred into a reaction tube and reduced to elemental mercury with stannous sulfate in hydroxylamine sulfate-sodium chloride solution. After 40 s, compressed air was used to purge the mercury vapour through a three-way stopcock to the spectrophotometer for measurement.

Detection limits were 20 $\mu g \cdot kg^{-1}$ for PCB (4:1 Aroclor 1254:1260 standard), 5 $\mu g \cdot kg^{-1}$ for mirex and DDT, 1–2 $\mu g \cdot kg^{-1}$ for the other organic contaminants, and 5 $\mu g \cdot kg^{-1}$ for mercury. Residue levels for substances such as DDT and chlordane that contained several products that were present in relatively high concentrations were reported as p,p'-DDE and Σ DDT, and α- and Σ chlordane. Substances whose average concentrations were less than 10 $\mu g \cdot kg^{-1}$ and were not detectable in 50% of the samples tested were not reported. Samples which included some concentrations that were below the detection limit were assigned a concentration that was 50% of the detection limit for computational purposes.

Lipid content was determined by extracting a 5-g sample with 100 mL of 1:3 methylene chloride:hexane. The mixture was blended, then filtered to remove the particulate materials. The solvent fraction was then transferred to beakers and placed in a fume hood at 30°C until constant weight was attained.

The effects of spawning on the kinetics of contaminants were examined according to the following procedure. Changes in contaminant levels cannot be entirely explained on the basis of differences in concentrations observed between fish and eggs alone. Any changes should be estimated by converting the relative concentrations ($\mu g \cdot kg^{-1}$) to absolute levels (micrograms per fish) to eliminate the bias of weight (Niimi and Cho 1981). Contaminant levels in fish and eggs were examined on the basis of the micrograms of each substance present in the eggs and pre- and post-spawning fish. After calculating the absolute amount of residue that could be eliminated through spawning, residue levels were again expressed as relative levels.

Intra- and inter-specific relationships among weight, lipid, and contaminants parameters were examined for statistical significance using the regression equations $Y = a + bX$, $Y = a_e{}^{bX}$, and Log Y = Log a + bLog X. The equation of best-fit, determined by the correlation coefficient, was reported for each data set.

Results

There were interspecific differences in lipid content and

TABLE 2. Contaminant levels in gravid fish, eggs, and fish without eggs among the species examined. The values represent the mean and standard deviation of concentrations for each substance.

	Substance $\mu g \cdot kg^{-1}$												
	PCB	*p,p'*-DDE	Σ DDT	α chlordane	Σ chlordane	Mirex	Heptachlor epoxide	Dieldrin	HCB	Lindane	Endrin	Endosulfan	Mercury
							Rainbow trout (n=9)						
Fish with eggs (A)	4810±1420	784±304	1321±498	146±47	191±58	212±69	14±15	42±22	24±6				236±57
Eggs	2050±700	293±97	458±149	61±18	76±25	71±29	2±1	20±9	14±7				11±8
Fish less eggs (B)	5249±1590	872±345	1476±548	159±53	210±65	229±83	16±17	48±27	26±6				280±69
% B/A (means)	9.1	11.2	11.4	8.9	10.0	10.8	14.3	14.3	8.3				15.3
							White sucker (n=9)						
Fish with eggs (A)	3390±1223	233±139	531±293	131±57	150±59	44±25	9±4	32±23	12±5				89±34
Eggs	1920±717	115±67	273±179	64±51	76±54	24±16	8±6	25±20	11±5				9±4
Fish less eggs (B)	3699±1338	258±155	585±323	146±61	166±63	48±28	8±4	35±27	12±6				106±41
% B/A (means)	9.1	10.7	10.2	11.4	10.7	9.7	—	9.4	—				16.0
							White bass (n=8)						
Fish with eggs (A)	2126±758	71±19	214±61	70±9	88±10		7±3	9±9	3±2	20±4	8±4	16±14	102±36
Eggs	2302±869	68±21	212±80	73±22	91±24		5±3	10±10	6±2	20±5	9±8	9±11	4±2
Fish less eggs (B)	2115±788	71±20	213±62	69±10	88±11		7±3	5±4	3±2	19±4	8±4	16±16	111±40
% B/A (means)	−0.5	0	−0.5	−1.4	0		0	—	—	−5.0	—	0	10.9
							Smallmouth bass (n=8)						
Fish with eggs (A)	2451±1437	77±51	292±151	51±14	82±48		13±5	16±9	4±3	9±3	43±22	34±21	188±114
Eggs	2862±1548	229±284	682±557	102±38	156±66		14±12	18±12	9±6	21±4	47±36	67±52	8±3
Fish less eggs (B)	2396±1504	65±36	273±116	47±14	76±48		12±5	21±12	4±3	9±3	42±22	32±21	199±125
% B/A (means)	−2.2	−15.6	−6.5	−7.8	−7.3		−7.7	31.2	—	0	−2.3	−5.9	5.5
							Yellow perch (n=8)						
Fish with eggs (A)	639±821	36±21	158±39	41±10	58±16		2±2	6±6	3±2	11±5	19±23	16±20	52±15
Eggs	766±967	42±19	154±101	42±22	58±18		2±2	5±6	4±2	12±7	11±14	9±10	5±4
Fish less eggs (B)	608±788	37±25	163±56	41±13	58±18		2±2	13±14	3±2	11±6	21±26	19±23	67±21
% B/A (means)	−4.8	2.8	3.2	0	0		—	—	—	0	10.5	18.8	22.4

TABLE 3. Percent of residue levels monitored in fish that were distributed in the eggs. The mean and standard deviation of the percent transferred for each substance, and the mean of means for the organic contaminants are shown for each species.

	Percent of substance in eggs				
Substance	Rainbow trout (n=9)	White sucker (n=9)	White bass (n=8)	Smallmouth bass (n=8)	Yellow perch (n=8)
PCB	5.4±1.8	10.0±2.7	9.2±2.4	10.2±5.7	29.3±11.2
p,p'-DDE	5.4±2.2	9.0±2.8	8.8±2.1	18.5±8.5	30.3±18.8
Σ DDT	4.9±1.8	9.4±3.8	9.0±2.4	16.9±6.8	22.1±14.8
α chlordane	6.0±1.8	8.4±5.1	9.5±2.3	14.5±5.9	23.5±13.4
Σ chlordane	5.6±1.9	8.9±4.8	9.3±2.3	15.9±6.9	23.1±14.7
Mirex	4.5±1.2	9.5±2.9			
Heptachlor epoxide	2.9±2.9	28.0±9.5	6.3±3.8	8.3±5.4	31.0±22.8
Dieldrin	7.1±3.8	15.4±6.2	8.0±5.6	10.4±10.0	22.6±16.5
HCB	7.8±3.7	21.3±15.9	22.3±20.6	18.0±6.1	34.5±13.5
Lindane			9.4±2.0	17.6±5.6	24.3±10.6
Endrin			12.5±9.9	9.4±7.3	20.8±20.5
Endosulfan			9.7±16.5	14.9±10.3	18.8±15.4
Mercury	0.6±0.4	1.8±0.8	0.3±0.2	0.4±0.4	2.3±1.8
Mean of means for organic substances	5.5±1.4	13.3±7.0	10.4±4.2	14.0±3.8	25.5±5.0

TABLE 4. Regression analyses among egg weight and lipid content on the mean of means of the percent organic contaminants transferred from females to eggs for the five species examined. All relationships are statistically significant at the $P < 0.01$ level.

Relationship	Equation	r^2	F-value
% lipid in whole fish vs. mean of residues	$\text{Log } Y = 2.533 - 1.691 \text{ Log } X$	0.94	43.32
% of total lipid in eggs vs. mean of residues	$Y = -2.736 + 1.016X$	0.91	31.11
% lipid in whole fish vs. % lipid in eggs	$\text{Log } Y = 2.169 - 1.116 \text{ Log } X$	0.79	11.34
% eggs of total weight vs. % lipid in eggs	$\text{Log } Y = 1.713 - 0.723 \text{ Log } X$	0.89	23.68

egg weight among the five species examined (Table 1). In most cases, these parameters were not significantly influenced by body weight over the range tested. Mean lipid content of gravid fish ranged from 5.1% for yellow perch to 11.4% for rainbow trout. Percent lipid increased significantly with body weight for yellow perch ($P \lesssim 0.05$), but not the other species. Mean egg weight ranged from 7.4% of total weight for smallmouth bass to 22.3% for yellow perch. This percentage increased significantly with body weight for white sucker and smallmouth bass ($P \lesssim 0.05$), but not for rainbow trout, white bass, or yellow perch. The percent of total lipid deposited in eggs of each species ranged from 9.7% in white bass to 27.1% for yellow perch.

Up to 11 organic contaminants or their metabolites, and mercury, were monitored in fish and eggs (Table 2). Ten substances were measured in rainbow trout and white suckers collected from Lake Ontario and 12 substances in fish from Lake Erie. Concentrations of PCB, DDT, and chlordane were proportionally higher than those of the other organic contaminants in all species from both lakes. Mirex was detectable only in fish collected from Lake Ontario.

There were some relative differences in residue levels between fish and eggs among the species. Concentrations of most organic contaminants in gravid rainbow trout and white suckers were about 10% higher than what was found in their eggs, whereas levels in gravid smallmouth bass were about 5% lower than those of its eggs. There were little or no differences in residue levels between whole body and eggs in gravid white bass and yellow perch. The response of mercury was unlike that of the other substances. There were differences in whole body mercury levels among the species, but levels in eggs were substantially lower than in whole body and were similar among the species.

Contaminant transfer was estimated as the percent of total amount of each substance deposited in eggs. On a comparative basis, the percentages of organic contaminants present in eggs showed less variation for a given species than the percentages of the different substances among the five species (Table 3). The grand mean for the percent of organic contaminants in fish that were deposited in eggs for each species ranged from 5.5% for rainbow trout to 25.5% for yellow perch. The means for rainbow trout and yellow perch were

significantly different ($P \lesssim 0.05$) from the other three species which did not differ significantly among themselves. The relationship for mercury was less well defined because the concentrations in eggs were low for all species.

The interrelationships among weight and lipid ratios were examined to determine which parameters significantly influenced the distribution of organic contaminants. Regression analyses among the five species suggested that the distribution was significantly influenced by the percent lipid in fish and percent of total lipid deposited in eggs ($P < 0.01$), but not necessarily by the percent lipid in eggs or percent egg of total weight (Table 4). Percent lipid content of eggs was significantly influenced by the percent lipid in the fish and percent egg of total weight (<0.01), but not the percent of total lipid in eggs. The latter parameter was not influenced by the percent egg of total weight or the percent lipid in the fish.

Discussion

This study has demonstrated that factors like percent lipid in fish and percent of total lipid deposited in eggs can influence the transfer of contaminants from fish to eggs. An excellent agreement ($r^2 = 0.9$) was attained among the regression equations that described these relationships. Based on these observations, it is suggested that reliable estimates of contaminants transfer from fish to eggs can be predicted for other species whose lipid levels are comparable to those examined in this study. Specific information that would be required for these species are contaminant levels in fish and lipid content in fish and eggs.

The toxicological effects contaminants may have on eggs at the concentrations observed are difficult to assess because of the limited information available on the effects of individual substances and their possible synergistic response. Comparison of contaminant levels in eggs reported herein with those reported for fertilized eggs may require a two- to three-fold weight adjustment to account for the increase in weight due to water uptake during the post-fertilization hardening process. If this weight adjustment is considered, the data suggest the residue levels monitored in this study could have detrimental effects on egg and fry survival of rainbow trout and possible effects on the other species based on the following observations. Hogan and Brauhn (1975) reported rainbow trout eggs which contained 0.33 $mg \cdot kg^{-1}$ Aroclor 1254 incurred 10–28% mortalities, and 60–70% of the fry were deformed after 30 d posthatch. Johansson (1970) reported 46–100% mortality in fertilized eggs and fry of Atlantic salmon (*Salmo salar*) whose PCB levels ranged from 0.6 to 1.9 $mg \cdot kg^{-1}$ on a wet weight basis and 14.4–34.0 $mg \cdot kg^{-1}$ on a lipid basis. DDT was not detectable in most samples. A reanalysis of the salmon data also indicated a significant increase in mortality with increasing PCB levels ($P \lesssim 0.05$). Zitko and Saunders (1979) reported 79.8–91.4% hatching success in Atlantic salmon whose eggs contained 1.9–6.5 mg Aroclor 1254 per kilogram lipid. For comparison, mean PCB levels in eggs observed in this study were estimated to be 23.6, 33.7, 23.7, 21.4, and 13.2 $mg \cdot kg^{-1}$ lipid for rainbow trout, white sucker, white bass, smallmouth bass, and yellow perch, respectively. PCB levels of these eggs on a fertilized, wet weight basis could range from 0.3 to 1.5 $mg \cdot kg^{-1}$.

TABLE 5. Influence of spawning on relative changes in fish weight and contaminants concentrations among the five species examined.

Species	Percent change in measurements attributed to spawning		
	Weight	Organic contaminants	Mercury
Rainbow trout	−13.6	+≈10	+15.3
White sucker	−17.6	+≈10	+16.0
White bass	−8.4	No change	+10.9
Smallmouth bass	−7.4	−≈5	+5.5
Yellow perch	−22.3	Slight change	+22.4

A similar analysis based on the studies of lake trout suggests the levels of PCB and Σ DDT monitored in Lake Ontario rainbow trout may not be acutely toxic to lake trout although contaminant-related mortality is evident. Studies conducted primarily at the Great Lakes Fishery Laboratory, Ann Arbor, MI, between 1972 and 1977 suggested the levels of PCB and Σ DDT in water and biota of Lake Michigan during the early 1970s were sufficient to affect the survival of lake trout fry hatched in the lake (Wilford et al. 1981). Concentrations of PCB and Σ DDT exceeded 10 $mg \cdot kg^{-1}$ in adult fish and 4 $mg \cdot kg^{-1}$ in eggs. Subsequent studies on lake trout eggs which contained 3.6–11.1 $mg \cdot kg^{-1}$ PCB and 2.5–7.2 $mg \cdot kg^{-1}$ DDT reported survival rates of 40.3–65.5% (Mac et al. 1981). No significant correlation could be demonstrated between survival rate and PCB and DDT concentrations and it was concluded that hatching success may have been related to differences in incubation temperatures. Concurrent studies also examined the survival of fry which contained average levels of 3.8 $mg \cdot kg^{-1}$ PCB and 2.1 $mg \cdot kg^{-1}$ DDT. Fry exposed to waterborne PCB and DDE at concentrations 1–25 times above that found in the waters of southeastern Lake Michigan incurred mortalities of 40.7–46.5% whereas mortalities among the control group averaged 21.7% after 176 d (Berlin et al. 1981). These studies reported mortalities of lake trout eggs and fry which contained PCB and Σ DDT in the low $mg \cdot kg^{-1}$ in excess of 40%, although it was postulated that other factors may have contributed to the mortality. Nevertheless it could be suggested that the levels of residues monitored contributed to the relatively high mortality rates observed.

Toxicological studies on DDT suggest the levels monitored in this study would not have an appreciable effect on hatching success or fry survival. Most studies suggest that concentrations of 2–4 $mg \cdot kg^{-1}$ are required to cause 10–20% mortalities, and 10 $mg \cdot kg^{-1}$ for mortality rates in excess of 50% in salmonids (Burdick et al. 1964; Macek 1968; Berlin et al. 1981).

Spawning could have a significant effect on the kinetics of environmental contaminants in fish (Table 5). This is due to changes in weight and residue levels which are attributed to egg deposition, and to differences in residue concentrations between fish and eggs. Assuming nearly all the eggs in the ovaries are deposited, postspawning weight loss could be estimated from the ovary weight. The changes in contaminant levels may not be as clearly defined as changes in weight. Organic contaminant concentrations in gravid fish whose

whole body levels are similar to those of their eggs, which would include species such as white bass and yellow perch, would not change appreciably following egg deposition because residue losses would be proportional to weight losses (Table 2). Species such as rainbow trout and white sucker whose residue concentrations in eggs are substantially lower, would show an increase in residue concentrations because residue losses through eggs would be lower in proportion to weight losses. In contrast, species like smallmouth bass whose residue concentrations in eggs are higher than those of the fish, would show a decrease in concentrations following spawning because residue losses through eggs would be higher in proportion to weight losses. Mercury concentrations would show a significant increase because levels in eggs are substantially lower than those in fish. Overall, the extent of change in residue concentrations will vary with species and would be directly proportional to the differences in relative concentrations between fish and eggs and the percent of body weight that is deposited as eggs. This relationship would not be applicable to males because the amount of semen released would represent only a small fraction of body weight and changes in contaminant concentrations may not be detectable.

Studies which have examined the distribution of organic contaminants in fish report concentrations can vary among tissues and organs (Guiney et al. 1979) with species (Guiney and Peterson 1980), which can change seasonally (Reinert and Bergman 1974; Olsson et al. 1978). The similarities among the percentages of organic contaminants distributed in females and eggs were consistent for a given species for each of the five species examined in this study. One hypothesis that could explain this response is that there is little or no selection for one group of substances to be mobilized in preference to another and the organic contaminants are uniformly distributed within the lipid complement of a fish. However, further studies would be required to examine this hypothesis. These studies should preferably be designed to examine a spectrum of organic contaminants in a variety of species.

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Paralytic Shellfish Poison in Sea Scallops (*Placopecten magellanicus*) in the West Atlantic

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JAMIESON, G. S., AND R. A. CHANDLER. 1983. Paralytic shellfish poison in sea scallops (*Placopecten magellanicus*) in the west Atlantic. Can. J. Fish. Aquat. Sci. 40: 313 – 318.

Levels of *Gonyaulax excavata* toxin in sea scallop (*Placopecten magellanicus*) tissues were monitored in eastern Canada on a monthly basis between 1977 and 1981. All tissues but the adductor muscle were found to be highly toxic in Bay of Fundy scallops, with negligible toxicity observed in scallops from Georges Bank, the outer Scotian Shelf, and Northumberland Strait scallops. Level of Bay of Fundy toxicity was much higher than previously observed (maximum digestive gland toxicity: 150 000 μg/100 g in March 1978), and recent average monthly toxicity for Bay of Fundy scallop roe ranged from 184 to 286 μg/100 g. Considerable fluctuation in toxicity can occur between adjacent months, and peak toxicities in sea scallops occur during fall and winter months. Scallop roe fisheries should be permitted to be established for scallops fished from the northern part of Georges Bank and Northumberland Strait. However, a closed zone for scallop roe should be established in the Bay of Fundy and adjacent Scotian Shelf.

Key words: scallop, PSP, *Gonyaulax*, *Placopecten*, mollusk

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Entre 1977 et 1981, on a suivi, sur base mensuelle, les niveaux de toxine de *Gonyaulax excavata* dans les tissus du pétoncle géant (*Placopecten magellanicus*) dans l'est du Canada. On a constaté que tous les tissus, sauf le muscle adducteur, étaient fortement toxiques chez les pétoncles de la baie de Fundy, alors que la toxicité de ceux du banc Georges, de l'extérieur du plateau Scotian et du détroit de Northumberland était négligeable. Les niveaux de toxicité dans la baie de Fundy étaient de beaucoup supérieurs à ceux observés antérieurement (toxicité maximale de la glande digestive : 150 000 μg/100 g en mars 1978), et la toxicité mensuelle moyenne récente de la rogue de pétoncle de la baie de Fundy variait de 184 à 286 μg/100 g. Il peut se produire, d'un mois à l'autre, de fortes variations de toxicité, et les pics se produisent en automne et en hiver. On devrait permettre l'exploitation de cette espèce pour la rogue dans la partie septentrionale du banc Georges et dans le détroit de Northumberland. Cependant, il faudrait établir une zone interdite à l'exploitation de la rogue dans la baie de Fundy et sur le plateau Scotian avoisinant.

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SEA scallops (*Placopecten magellanicus*) from several west Atlantic commercial fishing areas were examined routinely to document toxicity levels of paralytic shellfish poisoning (PSP). Prakash et al. (1971) state that sea scallops are responsible for less than 1% of all recorded illnesses due to PSP, but this is largely because in North America usually only the adductor muscle of scallops is marketed commercially. Bourne (1965) reports that *Gonyaulax* toxins are concentrated in the digestive gland, and, whereas other organs may be toxic, the adductor muscle has no measurable concentration. This is not true for all scallop species, though, as the adductor muscle from the purple-hinged rock scallop, *Hinnites giganteus* has been shown to be toxic on occasion (2000 μg/100 g tissue: Anon. 1980). Shimizu and Yoshioka (1981) indicate that, although both foot and adductor muscle tissues of the sea scallop can reductively transform toxins and thus deactivate them, this ability is apparently confined to locomotor tissue and is not evident in other organs.

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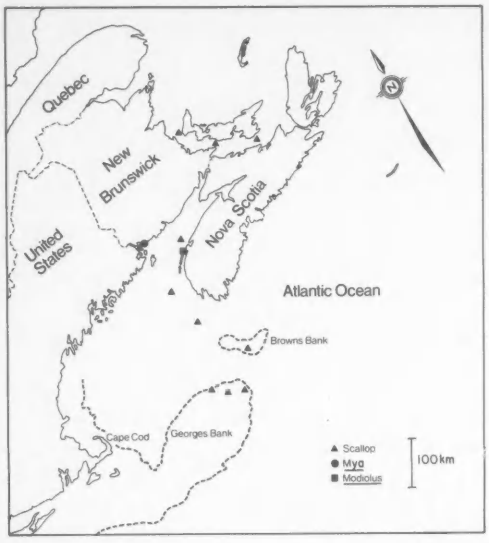

FIG. 1. Toxicity sample locations in the Canadian Maritimes, 1977–79.

Bourne (1965) investigated the seasonal variation in toxin level in different scallop organs from two scallop beds in the southwestern part of the Bay of Fundy, and determined summer toxin levels for scallop digestive glands from a number of stations on Georges Bank and in the Northumberland Strait. In the Bay of Fundy, the digestive glands and mantles were continually toxic, with lowest toxicity levels measured in February and April 1964. The gonad was occasionally slightly toxic (maximum level: 38 μg/100 g), whereas the gills and adductor muscle were always toxin-free (i.e. <32 μg/100 g). However, Medcof et al. (1947) reported a gill toxicity level of 2800 μg/100 g in May 1946. The digestive glands of Georges Bank and Northumberland Strait scallops during the summer were either toxin-free or only slightly toxic (Bourne 1965).

Recent interest shown in the development of a scallop roe industry by processors in Nova Scotia has prompted re-examination of seasonal levels of *Gonyaulax* toxin in sea scallops.

Methods

Live scallops were obtained from both the offshore and Bay of Fundy commercial scallop fisheries, as well as from monthly research sampling off Mascarene in Passamaquoddy Bay. Scallops were collected and held alive in seawater until the vessel returned to port (1 d maximum). They were processed alive and five major organs examined (digestive gland, gills, mantle, gonad, and adductor muscle). Each part was carefully separated to avoid its rupture and possible contamination of the other organs or tissues.

Unlike the procedure used by Bourne (1965) in which the dissected parts were washed and allowed to drain for 5 min before preparing extracts, our samples were placed directly into separate containers without rinsing. The tissues were kept cool until extracts could be prepared at the nearest Fisheries Inspection Laboratory. Extract preparation was the same as described by Bourne (1965), except that, when possible, 200 g of each tissue was used. Depending on relative organ weights, each sample constituted up to 30 animals.

Bioassays were carried out by the Laboratory of Hygiene, Health and Welfare Canada, Ottawa. (See Bourne (1965) for description of bioassay procedure.)

Results

Scallops collected offshore from the northern edge and northeast peak of Georges Bank (Fig. 1) showed insignificant toxicity (<32 μg/100 g) in all tissues but the digestive gland on all occasions. Low toxin concentrations in digestive glands (maximum: 140 μg/100 g tissue) were observed in May 1980, and in June 1981. No toxic scallop tissues have been found on the southwestern Scotian Shelf (Browns Bank, German Bank, Lurcher), but sampling was not extensive. As this geographic area borders the Bay of Fundy, a region where scallop toxicity is prevalent (Fig. 2), it would seem likely that some toxicity may exist in scallops from the Scotian Shelf, at least in that area of the Shelf proximate to the Bay of Fundy.

During the past several years scallop roe have been commercially landed and processed in the Northumberland Strait region of the Gulf of St. Lawrence. Fisheries Inspection Laboratories at Charlottetown and Shediac have monitored adductor muscles and gonads for PSP causing toxins, and found them to be consistently free of any toxins.

Of the five scallop tissues studied from scallops in the Bay of Fundy off Digby, N.S., the digestive gland was the most toxic, with a peak toxicity of 150 000 μg/100 g tissue recorded in March 1978 (Fig. 2). In the adductor muscle, a maximum toxin level of 60 μg/100 g was recorded in November 1977, but on all other occasions, toxicity in this tissue did not exceed 41 μg/100 g. Gill tissue was moderately toxic (100–600 μg/100 g) from October 1977 to February 1978, and in July 1979, August 1980, and July 1981. Otherwise, gill toxicity was <100 μg/100 g. In comparison with peak toxicity levels of whole, intertidal, horse mussels (*Modiolus modiolus*) (Fig. 3) collected at Fisheries Inspection Station, Nova Scotia No. 7 (Centreville), the seasonal timing of peak toxicity in scallop digestive glands was about 4–6 mo later. It is difficult to compare actual magnitude of toxin level between the two species, as horse mussel scores for individual tissues were not determined. However, the extremely high scallop digestive gland values would appear to make scallops a more toxic species if entirely consumed. On January 18, 1981, and on February 24, 1981, toxicities of whole Mascarene scallops were compared with those of the digestive gland alone: scores were 2200 and 25 000 μg/100 g, respectively, in January, and 2100 and 13 000 μg/100 g, respectively, in February.

In contrast to scallops off Digby, N.S., scallops collected off Mascarene, Passamaquoddy Bay, were generally less

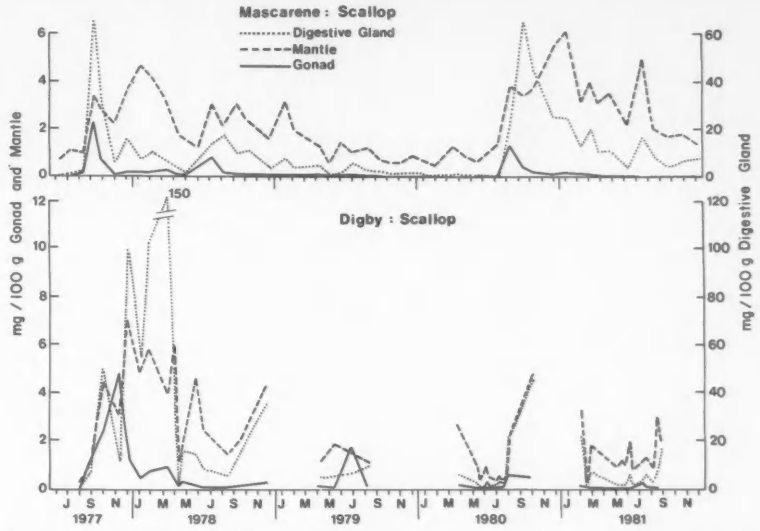
Mascarene : Scallop
Digestive Gland
Mantle
Gonad
mg / 100 g Gonad and Mantle
mg / 100 g Digestive Gland
Digby : Scallop
150
J S N J M M J S N J M M J S N J M M J S N J M M J S N
1977
1978
1979
1980
1981

FIG. 2. Seasonal toxicity scores for three scallop tissues from off Mascarene, Passamaquoddy Bay, and off Digby, N.S.

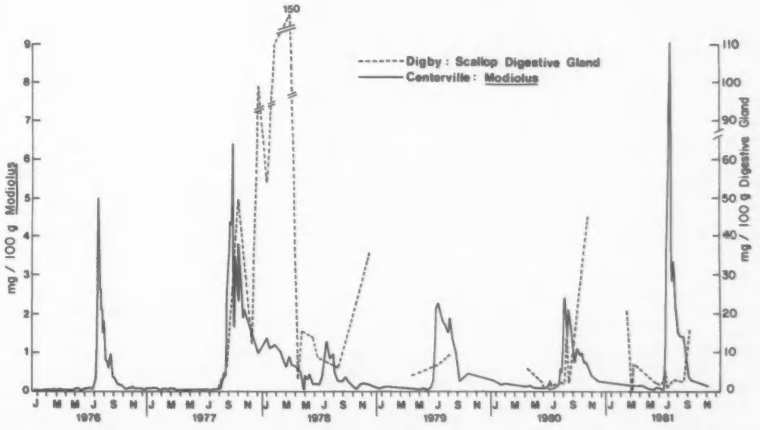
150
Digby : Scallop Digestive Gland
Centerville : Modiolus
mg / 100 g Modiolus
mg / 100 g Digestive Gland
J M M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M J S N
1976
1977
1978
1979
1980
1981

FIG. 3. Seasonal toxicity scores for scallop digestive gland and *Modiolus modiolus* in the Digby area of the Bay of Fundy.

toxic and had peak toxicities in both September 1977 (Fig. 2) and in September 1980 (digestive gland: 65 000 μg/100 g on both occasions). As with Digby scallops, the digestive gland was the most toxic tissue, followed by the mantle, gonad, gills, and adductor muscle, respectively. A maximum muscle toxicity of 120 μg/100 g was recorded in July 1978, but on all other occasions, muscle toxicity was negligible.

When Mascarene scallop toxicity was compared with the toxicity of whole, intertidal *Mya arenaria* (Fig. 4), fluctuations in toxicity appeared more closely correlated than was the scallop/horse mussel correlation off Digby, N.S. (Fig. 3). Toxicity of *Mya* from Fisheries Inspection Station, New Brunswick No. 14 (Scotchman's Cove), appeared to reflect more closely the toxicity levels of Mascarene scallops than did *Mya* from Fisheries Inspection Station, New Brunswick No. 15 (Letete), even though Letete is geographically closer to the scallop collection area. However, this latter sampling area does not completely drain at low tide, suggesting that microenvironmental variables may greatly influence toxicity magnitude.

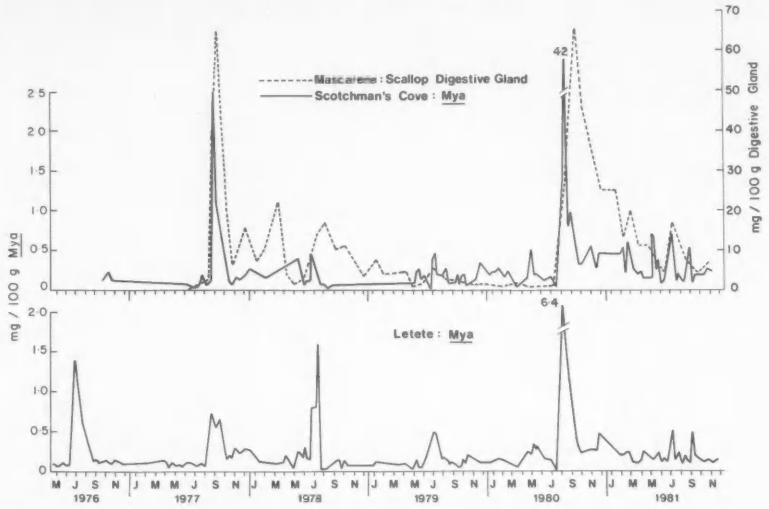
Mascarene : Scallop Digestive Gland
Scotchman's Cove : Mya
mg / 100 g Mya
mg / 100 g Digestive Gland
Letete : Mya
42
6·4
M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M J S N
1976
1977
1978
1979
1980
1981

FIG. 4. Seasonal toxicity scores for scallop digestive gland off Mascarene, and whole *Mya arenaria* (Boyd 1977, 1978, 1979) at Letete and Scotchman's Cove.

TABLE 1. Average monthly toxicities (μg/100 g tissue ± 1 SD) of scallop digestive glands and gonads in Bay of Fundy waters off (A) Mascarene, N.B., and (B) Digby, N.S.

Period	Average toxicity			
	n	Digestive gland	*n*	Gonad
A. Mascarene				
April 1963–March 1964[a]	12	1 070 (461)	12	32 (1)
June 1977–May 1978	12	13 942 (18 760)	11	387 (665)
June 1978–May 1979	10	7 536 (5 299)	10	140 (235)
June 1979–May 1980	10	2 015 (1 366)	9	35 (9)
June 1980–May 1981	11	21 900 (20 379)	11	240 (398)
B. Digby				
Aug. 1977–July 1978	11	48 475 (50 103)	11	1135 (1384)
Aug. 1978–July 1979	5	11 640 (13 359)	5	416 (723)
Aug. 1979–July 1980	5	4 300 (3 456)	5	64 (42)
Aug. 1980–July 1981	6	13 852 (16 843)	5	184 (201)

[a]From Bourne 1965.

Discussion

This study supports Bourne's (1965) observations that northeastern Georges Bank, Scotian Shelf, and Northumberland Strait scallops are essentially free of *Gonyaulax* toxins. However, in scallops from the Bay of Fundy (off Mascarene, N.B.), recent toxicity scores were much higher than those reported by Bourne (1965). White and Lewis (1982) present evidence that since 1974, *G. excavata* blooms in the Bay of Fundy, which occur between May and September, have been above average in intensity. Some inshore shellfish areas in the Bay of Fundy were closed during the 1980/81 winter; although not unprecedented, this has been uncommon since shellfish toxicity closures were initiated in 1943 (H. Boyd, Fisheries Inspection Laboratory, Black's Harbor, N.B., personal communication). This may explain the high toxicity of scallop gonad in our study, which is in contrast to the negligible toxicity of Bay of Fundy scallop gonads reported by Bourne (1965). It should be noted that the lowest concentration of poison that can be detected by the standard mouse test used in Canada is 32 μg/100 g of tissue (H. Boyd personal communication). Human sensitivity to poison varies considerably between individuals; many people may show symptoms of paralytic shellfish poisoning with a dose of 400–500 μg toxin, and with a dose of 2 000 μg toxin, some fatalities may occur (H. Boyd personal communication).

Average monthly digestive gland and gonad toxicities (Table 1) for Mascarene scallops indicate that although peak toxicities for digestive gland tissue were recorded in both September 1977 and September 1980 (Fig. 2), the year 1980/81 had the highest recent level of average monthly scallop toxicity. In contrast, scallops during 1979/80 had the lowest average monthly toxicity in recent years, demonstrating that a major change in average toxicity level can occur between consecutive years.

Bourne (1965) found that scallop toxicity in Bay of Fundy waters immediately outside Passamaquoddy Bay was higher than that inside Passamaquoddy Bay. Toxicity scores in this study were greatest in the Bay of Fundy off Digby, N.S., with a maximum digestive gland toxicity of 150 000 μg/100 g tissue in February 1978. In contrast to Mascarene, off Digby, N.S., 1977/78 had scallops with the highest average monthly toxicity (Table 1), although bias may exist because of infrequent winter sampling during the years 1978–81.

The biological mechanism leading to scallop toxicity appears largely related to the life cycle of *Gonyaulax*. In the fall, thick-walled, nonmotile, overwintering, resting cysts, termed

hypnozygotes (White and Lewis 1982), are formed. These cysts apparently settle to the sea bottom, and in deep water or other sheltered locations may accumulate for years (Anderson and Wall 1978). Excystment may be triggered by temperature change (Anderson 1980; Anderson and Morel 1979) but in the Bay of Fundy, how frequently this occurs and what percentage of the cysts present actually excyst each year is unknown. There is debate as to how toxic cysts are relative to the motile stage. (Dale et al. 1978; White and Lewis 1982), but it appears that they are at least of equal toxicity (White and Lewis 1982).

Medcof et al. (1947) noted that, unlike other shellfish, scallops retained their toxicity for extended periods. Bourne (1965) and this study indicate that sea scallops are most toxic in the fall and winter, in contrast to other shellfish and when *Gonyaulax* blooms were not evident. Deepwater scallop toxicity has been previously suggested to come from ingestion of cysts (Bourne 1965; Yentsch and Mague 1979). Is the distribution of high cyst densities then correlated with the distribution of toxic scallops?

Recent data on the distribution and abundance of cysts (Lewis et al. 1979; White and Lewis 1982) suggests a broad distribution of cysts at high densities in the sediment in deepwater areas off the Maine coast and in the Bay of Fundy. Abundance of cysts in the sediment was relatively low in locations where commercial quantities of scallops are found, i.e. 3–24 km off Digby Neck and Digby Gut, around southern Grand Manan Island, and in the deeper water areas between the islands in Passamaquoddy Bay, but this does not necessarily mean cysts were not present. The sampling method used by White and Lewis (1982) was recognized by them to be unreliable in sampling sandy or gravelly sediments in a quantitative manner, and this is the substrate type most frequently correlated with high scallop abundance (Jamieson unpublished data). It is possible that cyst occurrence on scallop grounds was underestimated.

Scallops are also most often found in commercial quantities in areas of significant tidal or wind-generated currents (Jamieson et al. 1981). Cysts may not permanently settle out of the water column in areas of strong currents and the feeding of filter feeders is enhanced when currents resuspend settled organic material. It would be expected that highest levels of scallop toxicity might be in areas where permanent sediment and cyst deposition was least.

Hsu et al. (1978) have analyzed the paralytic shellfish poison of Bay of Fundy sea scallops, and in contrast to local *M. arenaria*, scallops were found to contain a high concentration of neosaxitoxin, which in vitro studies indicated could be converted to saxitoxin, a principal toxin of *Mya*. The possibility of rapid biotransportation, or detoxification of toxins, may be important in explaining how scallops are able to function physiologically with such high toxin levels. Highly toxic scallops (>100 000 μg/100 g) do not gape or appear to show other evidence of altered metabolism (R. A. Chandler unpublished data) whereas mussels, *Mytilus edulis*, show physiological effects at concentrations of 12–15 000 μg/100 g (J. Medcof, St. Andrews, N.B., personal communication). This supports Shimizu and Yoshioka's (1981) observation that scallops may maintain toxins at low concentration by chemical detoxification while they are in sensitive body tissues. The physiological sensitivity of scallop nonlocomotor tissue to high toxin levels and possible ecological implications remain unknown.

In summary, scallop roe from the northern part of Georges Bank and Northumberland Strait are sufficiently free of *Gonyaulax* toxins to permit establishment of a scallop roe fishery. However, Bay of Fundy scallop roe can be very toxic, and routine monitoring should be established, with particular attention devoted to defining a closed zone in the Bay of Fundy and the nearby Scotian Shelf to ensure that no toxic tissues are processed for human consumption.

Acknowledgments

The support of the Black's Harbour, Yarmouth, and Halifax Fisheries Inspection Laboratories, and the Laboratory of Hygiene, Health and Welfare Canada, in extract preparation and analysis, is gratefully acknowledged. Mr Wellington Halliday and Mr Ian Marshall collected the material for most of the Digby/Yarmouth samples and Mr Terry Decker and Mr Ron Duggan collected the Lunenburg/Riverport material. Drs F. Bernard, N. Bourne, and A. White kindly reviewed the manuscript.

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Primary Productivity in a Large, Temperate Lake with River Interflow: Kootenay Lake, British Columbia

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JASPER, S., E. C. CARMACK, R. J. DALEY, C. B. J. GRAY, C. H. PHARO, AND R. C. WIEGAND. 1983. Primary productivity in a large, temperate lake with river interflow: Kootenay Lake, British Columbia. Can. J. Fish. Aquat. Sci. 40: 319 – 327.

Phytoplankton productivity in a large, deep lake with river interflow was determined using an incubator method modified to include vertical distributions of chlorophyll and temperature together with continuous surface irradiance measurements. The annual average areal production, in 1977, was 170 g $C \cdot m^{-2}$ with daily areal productions ranging from 100 to 2800 mg $C \cdot m^{-2}$. P_{max} for all samples correlated well with chlorophyll *a* ($r = 0.79$). No large horizontal trends in areal productivity or P_{max} were found in the lake at any time of the year. However, pronounced differences with depth in the photosynthetic characteristics of populations within the euphotic zone were common during the stratified season. The two large inflowing rivers are thought to be important to the productivity of Kootenay Lake as they initiate the spring production peak and supply nutrients to the deeper phytoplankton populations during the summer and fall period.

Key words: phytoplankton, productivity, incubator, riverine lake, vertical structure

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La productivité phytoplanctonique d'un grand lac profond, avec arrivée d'eau de rivière, a été déterminée par une méthode à incubateur modifiée de façon à inclure les distributions verticales de la chlorophylle et de la température, en même temps que des mesures continues d'irradiance en surface. La production moyenne annuelle était en 1977 de 170 g $C \cdot m^{-2}$, la production quotidienne par aire variant de 100 à 2 800 mg $C \cdot m^{-2}$. Il y a bonne corrélation entre le P_{max} de tous les échantillons et la chlorophylle *a* ($r = 0,79$). En aucun temps de l'année observe-t-on de fortes tendances horizontales de productivité ou de P_{max} dans le lac. Cependant, des différences marquées, en fonction de la profondeur, des caractéristiques photosynthétiques des populations dans la zone euphotique sont communément observées durant la saison de stratification. On croit que les deux grands tributaires sont un important facteur de productivité du lac Kootenay puisqu'ils déclenchent le pic de production printannière et fournissent des nutriments aux populations phytoplanctoniques des profondeurs en été et en automne.

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KOOTENAY Lake is a large (length 107 km, mean width 3.8 km), deep (maximum depth 154 m, mean depth 94 m), intermontane, temperate lake in southeast British Columbia (49°40′N, 116°50′W). The Kootenay River enters the extreme south end of the lake (Fig. 1) and the Duncan River enters the extreme north end. Together these rivers provide, on average, about 800 $m^3 \cdot s^{-1}$ of flow, resulting in a relatively short bulk residence time of ~1.5 yr (Wiegand et al. 1982). The lake's outlet is near its midpoint, through the West Arm, which conveniently divides the main part of the lake into the North and South Arms.

The riverine effects on the seasonal circulation patterns of Kootenay Lake relate primarily to changes over time in the depth of interflow of river water through the lake (Daley et al. 1981; unpublished data available from authors). At the start of the phytoplankton growing season (April) and subsequent to spring overturn, the rivers enter as warm surface overflows and help to stratify the water column. In summer, as lake surface temperatures rise, the inflowing rivers move through the lake as interflows, typically just above the main thermo-

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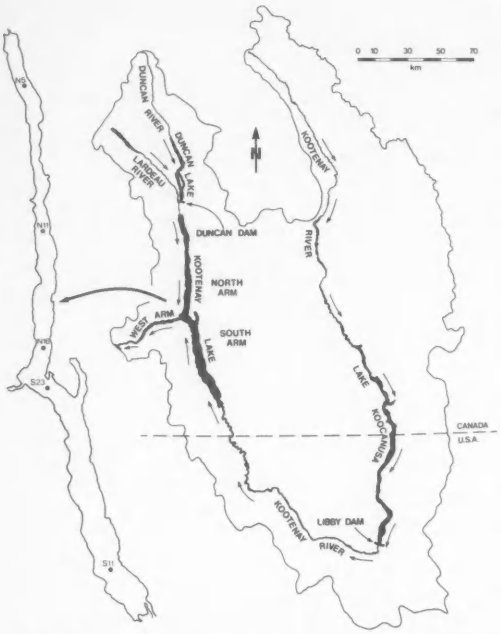

FIG. 1. Kootenay Lake, its drainage basin, and sampling stations in 1977.

cline, at depths between 10 and 30 m. At this time of year periodic heating during calm, sunny weather produces shallow, thermally stratified layers between the 0- and 12-m depths and above the riverine interflows. These thermal layers are transient, being easily broken down during storm events. During the autumn, and towards the end of the active growing season (October), the river interflows generally remain above the main thermocline but at progressively greater depths as the rivers and lake surface cool.

Northcote (1973) provided evidence that the highly turbid inputs from the Kootenay River were responsible for suppressing primary productivity in the South Arm of the lake. Since his 1964 study, however, the physical and chemical characteristics of both the major inflowing rivers have been altered considerably by the construction of dams upstream of the lake (Daley et al. 1981). Postimpoundment studies have shown that the rivers play a major role in controlling seasonal circulation patterns (Daley et al. 1981) and also in supplying nutrients to the summer epilimnion (Carmack and Gray 1982). This paper reports on a postimpoundment study of the phytoplankton productivity conducted in 1977, and examines the extent to which the riverine flows now influence the lake's productivity.

Methods

Experimental Design

The difficulties of using in-situ ^{14}C techniques for detailed studies of phytoplankton productivity, especially in open oceans and large lakes, have been well documented (Vollenweider 1965, 1970; Fee 1973a; Gargas et al. 1976). For example, there are logistical problems in sampling several, widely spaced stations in a short period of time and difficulties in extrapolating from short-term incubations to daily, seasonal, and annual values.

The use of incubators (Fee 1969, 1973a; Gargas 1976; Head 1976) to define the relationship between primary productivity and light intensity ($P(I)$), together with mathematical models that include measurements of light extinction coefficients and surface irradiance, have provided a more realistic estimate of daily and longer term rates. However, these procedures often assume, for simplicity, a vertically homogeneous euphotic zone. For Kootenay Lake there was evidence that this assumption would not be valid. Preliminary investigations, for example, identified river interflows and transient thermoclines within the euphotic zone, thus suggesting vertical heterogeneity.

Fee (1973b) addressed this problem of vertical heterogeneity by dividing the euphotic zone into as many layers as required and determining $P(I)$ curves for each layer. In this way vertical changes in biomass, or photosynthetic characteristics, could be accommodated. One problem with this approach is the effort involved in producing each $P(I)$ curve; increasing the number of layers for each station inevitably results in a decrease in the number of stations that can be sampled. In situations where biomass levels show large fluctuations with depth, utilizing the $P(I)$ relationship to monitor these fluctuations becomes tedious.

To overcome the logistical problems of producing many $P(I)$ curves for each station, we modified Fee's incubator technique by incorporating chlorophyll and temperature profiles into the calculation procedure. In this way only two or three measurements of the $P(I)$ relationship are required (at selected depths within the euphotic zone) to describe vertical changes in photosynthetic characteristics. [These would be reflected as variations in the "shapes" of the $P(I)$ curves.] Close-interval measurements of chlorophyll and temperature throughout the water column are then used to modify the absolute magnitude of the $P(I)$ curves obtained at the selected depths thereby producing a $P(I)$ curve for each layer in the euphotic zone. These are then used in the calculation of daily areal productivities.

To provide productivity estimates for longer time frames (i.e. seasonal or annual values) the daily areal values between sampling dates are calculated using linearly interpolated profiles of chlorophyll, temperature, $P(I)$, and extinction, from the sampling dates, together with continuous measurements of surface irradiance.

In-Situ Measurements and Sample Collection

During 1977, five stations (Fig. 1) were monitored at 3- to 4-wk intervals. To select the depths for the $P(I)$ determinations, measurements were made first of the vertical temperature, conductivity, and turbidity distributions. The sampling depths were chosen to represent the various water types within the euphotic zone (the lower boundary defined as the depth to which 1% of surface light penetrates), and the num-

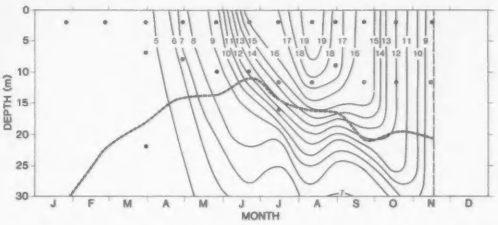

FIG. 2. Sampling schedule for 1977 showing $P(I)$ determinations at a typical station, S23, superimposed on the 0- to 30-m isotherms (°C). The depth of the 1% light level, representing the lower boundary of the euphotic zone, is shown as a broken line.

ber of samples collected was based upon the degree of vertical heterogeneity (Fig. 2). Usually two, but occasionally three, depths were selected for $P(I)$ measurements and six depths for chlorophyll *a* determinations.

At each station measurements were made of the extinction of photosynthetically active radiation (P.A.R.) with depth using a Licor underwater quantum sensor. Values were obtained at 1-m intervals from the surface to 15 m. The extinction coefficient was then determined from the linear slope of a plot of the natural log-transformed light values versus depth. On the few occasions when the transformed light profile deviated somewhat from a linear decrease with depth, the individual light values were used rather than the extinction coefficient. Continuous measurements were also taken of the surface P.A.R. irradiance using a Licor atmospheric quantum sensor located at the junction of the West Arm with the main lake (Fig. 1). Values were obtained at 10-min intervals throughout the year.

Water samples were collected using 8-L PVC Niskin bottles and placed in translucent or opaque (for productivity) plastic bottles. These were kept cool and transported back to the field laboratory within 1 to 3 h. A time-course experiment to measure changes in the $P(I)$ curve with storage showed no effects up to 4 h. Water samples were screened through 110-μm Nitex mesh to remove zooplankton, and aliquots were removed for chlorophyll *a*, adenosine triphosphate (ATP), phytoplankton species identification, and counts and $P(I)$ determinations.

Biomass and Productivity Determinations

Chlorophyll *a* was determined by 1-L filtrations through glass fiber filters (Reeve Angel 984H or Whatman GFF), extraction into 90% acetone using a Polytron homogenizer, and subsequent photometric analysis at 665 nm before and after acidification to correct for *a* pheopigments (Lorenzen 1967). ATP determinations followed the procedure of Holm-Hansen and Booth (1966) except that 0.45-μm Millipore filters and glycine buffer (pH 10) were used as recommended by Afghan (1977). ATPs were converted to living carbon biomass values using the ratio 1:250 (Holm-Hansen and Booth 1966). Phytoplankton species were identified and counted using the inverted microscope procedure of Utermöhl (1973). Measurement of individual species provided estimates of species cell volumes which were then combined with the count

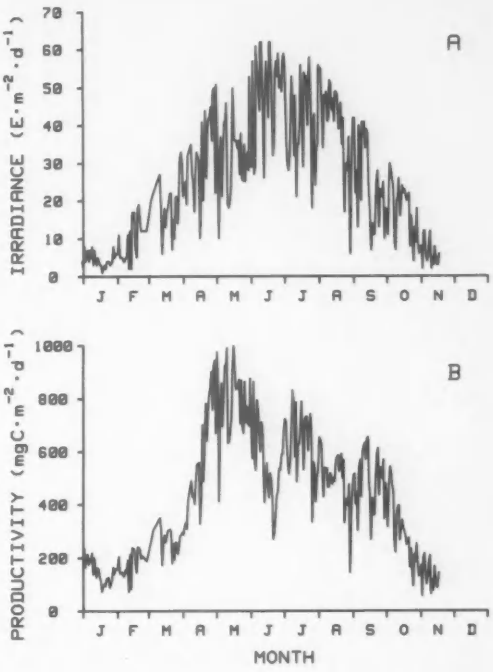

FIG. 3. Profiles for 1977 of (A) daily P.A.R. irradiance and (B) areal productivity at station S23.

data to determine the volumes of each species in the sample. These were then converted to fresh weight biomass values assuming a cell density of one.

Samples for $P(I)$ determinations were siphoned into prerinsed 60-mL glass bottles and injected with 1 mL of a stock $NaH^{14}CO_3$ solution. This stock was freshly prepared each day by filtering an ampoule of isotope (New England Nuclear) through a 0.45-μm Millipore filter and making up to a concentration of ~0.4 MBq·mL^{-1} using filter-sterilized, pH 8.5, deionized water. Duplicate bottles were then immediately placed in the incubator at each of four light intensities while a fifth pair was used as a "zero-time" blank correction (Morris et al. 1971). Our incubator design was based on that described by Shearer (1976) except that a larger and brighter light source, a 400-W metal-halide lamp and reflector (GTE Sylvania) was used. This lamp, with spectral distribution from 400 to 650 nm and a peak around 510 nm, provided a maximum light level of 1100 μE·m^{-2}·s^{-1} in the first chamber of the incubator. Attenuation of the light between the source and each chamber was accomplished by using neutral density screens. To determine the light level in each chamber a pair of incubation bottles was removed and replaced with the Licor underwater quantum sensor. An average of 12 measurements, throughout one revolution, was obtained. Incubator light levels were determined at regular intervals throughout the year, and whenever the screens or lamp were changed. Incubations were carried out usually within ±0.5°C

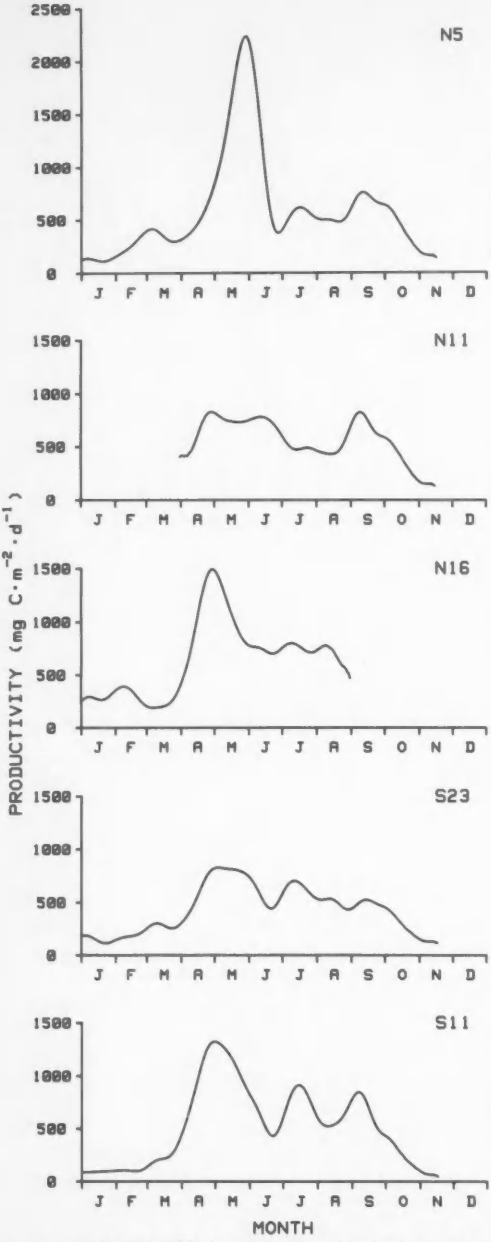

FIG. 4. Profiles for 1977 of "smoothed" areal productivities at the five lake stations.

of the temperature of the shallowest water sample from each depth series. Thus deeper samples which, in many cases, had

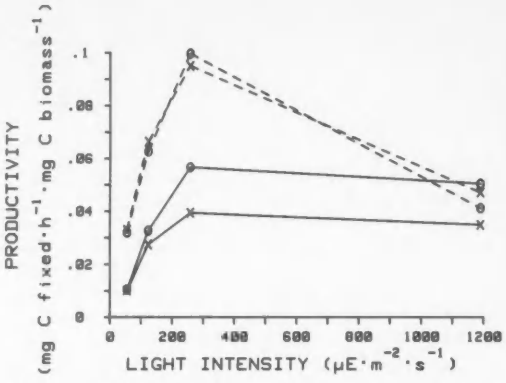

FIG. 5. Incubator productivity versus light curves, normalized for living carbon, showing typical vertical differentiation during the stratified period. S11 1 m (×—×), S11 12 m (×---×), S23 1 m (○—○), and S23 12 m (○---○), August 11, 1977.

lower in-situ temperatures, were incubated at elevated temperatures; the resulting enhanced productivities were adjusted by introducing a Q_{10} correction during computation.

Incubations lasted from 2 to 4 h. The incorporation of ^{14}C into the particulate phase together with labeled excretion products were determined using the acidification and bubbling method outlined by Schindler et al. (1972) but modified to permit bubbling of 8-mL aliquots within scintillation vials. Furthermore 1 mL of xylene was added before bubbling to prevent loss of labeled volatile organics during the 15- to 20-min bubbling period. Samples were counted, as a gel, by addition of 8 mL of Aquasol-2 cocktail (New England Nuclear). Counting efficiencies were determined periodically by internal standardization using [^{14}C]toluene. Total inorganic carbon was measured using an Oceanographic International infrared analyzer.

CALCULATION OF INTEGRAL PRODUCTIVITIES

As described by Fee (1973a, b) the incubator-produced $P(I)$ curves can be used together with light extinction measurements and surface irradiance values to produce a simulated in situ photosynthesis profile for each surface light value. Integration of these profiles over depth and time produces a daily areal rate.

Our procedure first normalizes the $P(I)$ curves with respect to their chlorophyll a content ($P\text{chl}(I)$). Then, by linear interpolation between two curves or extrapolation from the shallowest curve to the surface and the deepest curve to the bottom of the euphotic zone, produces a $P\text{chl}(I)$ curve for each 1-m depth interval within the euphotic zone. [Gaps in the chlorophyll a and temperature profiles are also filled by linear interpolation and extrapolation.] For each surface irradiance value (I_0), the light penetration to depth z (I_z) is calculated from:

$$I_z = (1 - R)\, I_0 e^{(-kz)}$$

where k is the extinction coefficient and R is the fraction of

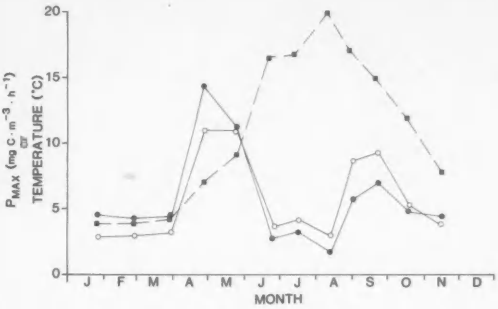

FIG. 6. Horizontal profiles of average lake surface temperature (■), P_{max} (○), and P_{max} normalized to 10°C using a Q_{10} of 2.1 (●), 1977.

P.A.R. quantum light lost by reflection at the lake surface and by absorption of the less penetrating wavelengths in the surface layers. The value of R was determined by comparison of the zero depth light value [obtained by extrapolating the extinction linear regression line] with the actual above-surface measurement of irradiance. An average value of 0.3 (n = 46) was used.

For each value of I_z the "instantaneous" productivity at depth z is calculated from the corresponding Pchl(I) curve multiplied by the chlorophyll a value at that depth. This productivity (P_i) is then corrected for the difference in temperature between the incubator and the lake by the use of a Q_{10} correction:

$$P = P_i \cdot Q_{10}^{(T_z - T_i)/10}$$

where T_z is the actual or interpolated lake temperature and T_i is the incubator temperature. We determined the value of Q_{10} by measuring the changes in P_{max} (the highest productivity determined in the incubator) from several samples incubated at three different temperatures, and obtained an average value of 2.1.

Productivities for each surface-irradiance value and depth interval are then summed over depth and time to produce the daily integral production. To calculate the daily integral productions between sampling dates the Pchl(I), temperature, and chlorophyll profiles together with the extinction coefficients are first linearly interpolated from the values determined for each sampling date. The continuous surface-irradiance profile is then used to estimate integral productivities for each day.

The computed annual records of areal productivity show a high degree of day-to-day variability superimposed on longer-term seasonal trends. Thus to aid the interpretation and comparison of these records the data was smoothed using a numerical filter. Several numerical methods are available to reduce these shorter-period or high-frequency fluctuations (Jenkins and Watts 1968; Otnes and Enochson 1972), and some allow for the selection of the frequencies of interest (Graham 1963). To examine long-term changes throughout the year, we selected a numerical filter that completely excluded periods less than 30 d while allowing 60-d-periods to pass.

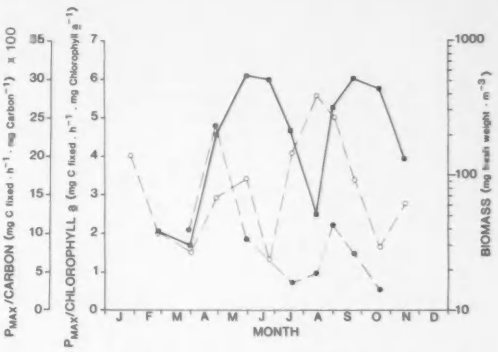
P_{MAX}/CARBON (mg C fixed · h^{-1} · mg Carbon^{-1}) × 100
P_{MAX}/CHLOROPHYLL a (mg C fixed · h^{-1} · mg Chlorophyll a^{-1})
BIOMASS (mg fresh weight · m^{-3})
MONTH
J F M A M J J A S O N D

FIG. 7. Horizontal profiles of average lake surface P_{max}/C (●), P_{max}/Chl a (○), and phytoplankton fresh weight biomass (■), 1977.

Results

AREAL PRODUCTIVITIES

Comparisons of areal productivities estimated by in-situ and incubator methods showed agreement within 15% on all occasions. There were small differences in the shapes of the depth profiles although no systematic pattern could be found. Inaccuracies in the measurement of ^{14}C uptake in both procedures, together with the use of only four measured points for each $P(I)$ curve (limited by our 4-chamber incubator), probably accounted for most of the discrepancies. The day-to-day changes in areal productivity, resulting from variations in surface light levels, were often large (Fig. 3). For example, areal production for station S23 was 890 and 411 mg C·m^{-2} on May 1 and 2, respectively. This illustrates the importance of using continuous light data in the calculation of areal primary productivity. Furthermore, the areal productivity profiles, after the filtering procedure was applied and the day-to-day fluctuations removed, clearly show the seasonal trends (Fig. 4).

The annual production of Kootenay Lake in 1977, averaged for all the stations, was 170 g C·m^{-2} with a mean daily value of 465 mg C·m^{-2}; ranging from less than 100 mg C·m^{-2}·d^{-1} to greater than 2800 mg C·m^{-2}·d^{-1}. The latter value, however, was atypical of the lake as a whole; a more representative maximum would be 1600 mg C·m^{-2}·d^{-1}.

The five stations had similar levels of annual productivity with no obvious trends from one end of the lake to the other. Annual productions ranged from 144 g·m^{-2} at S23 to 197 g·m^{-2} at N5. The seasonal curves generally show a rapid increase in areal productivities during April reaching a maximum later in the same month (Fig. 4). (N5, however, reached its maximum a few weeks after the other stations.) The differences in annual rates for each of the stations are primarily due to differences in the size of this spring peak. Two smaller peaks in July and September are also a common feature at all stations and together represent an equivalent production, on average, to the larger but shorter spring peak.

INCUBATOR MEASUREMENTS

$P(I)$ curves at all stations varied throughout the year in both

TABLE 1. Photosynthetic parameters determined from surface and lower euphotic zone samples collected during the thermally stratified season. No significant differences in species composition were observed for the shallow and deep samples on any of these dates.

Date	Station	Depth (m)	P_{max} (mg C·m^{-3}·h^{-1})	P_{max}/chl (mg C·h^{-1}·mg chl^{-1})	P_{max}/C (mg C·h^{-1}·mg C^{-1})
July 15	S23	1	5.47	5.70	0.059
		12	10.13	4.60	0.088
July 17	S11	1	3.43	4.29	0.009
		14	8.32	3.62	0.015
Aug. 11	S23	1	3.28	6.43	0.057
		12	7.47	5.34	0.10
Aug. 11	S11	1	1.97	6.16	0.039
		12	6.64	3.91	0.095

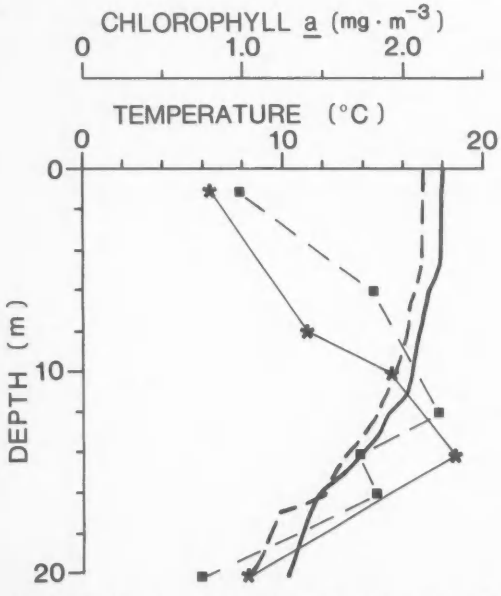

FIG. 8. Depth profiles of chlorophyll *a* at S11 (*—*) and S23 (■---■), together with temperature at S11 (—) and S23 (---), July 17, 1977, showing typical examples of heterogeneity during the summer period.

their shape and magnitude. Much of this seasonal lakewide variation can be explained by changes in biomass (i.e. living carbon) and temperature. No systematic differences in the $P(I)$ curves were seen between the five stations. However, at certain times of the year (June through August), the curves showed significant differences with depth at most of the stations. These differences became apparent after normalization of productivities with respect to living carbon and were observed even when temperature differences between the depths were less than 2°C (Fig. 5). Apparently this modest thermal stratification is sufficient to maintain populations with distinct photosynthetic characteristics.

P_{max} values ranged from 1.5 to 43 mg C·m^{-3}·h^{-1}. Lakewide surface values showed two maxima, one in May and the other in September, and minima in mid-summer and in winter (Fig. 6). Normalizing the P_{max} values for temperature further accentuates the difference in the two maxima (Fig. 6). Using the coefficient of determination, 62% of the variation in P_{max} and 68% of the variation in normalized P_{max} at all stations and depths could be explained by changes in chlorophyll *a* levels (n = 112). However, no significant correlation was found for P_{max} or normalized P_{max} with ATP (for both, r^2 = 0.003, n = 112).

The assimilation numbers (P_{max}/chlorophyll *a*) of all samples reached maximum levels in May and August (Fig. 7) coincident with, or shortly preceding, the periods of rapidly increasing phytoplankton fresh weight biomass (the latter measurements are included here simply as independent assessments of phytoplankton biomass). Low assimilation numbers occurred in June and October during peaks of biomass accumulation. No significant differences in assimilation numbers were found throughout the year between the two Arms of the lake. On any one date, however, values were often quite different within the euphotic zone. When this occurred higher assimilation numbers were usually found closer to the surface (Table 1). Although this was a general feature during the late spring to early fall period, at other times of the year variations with depth were not so pronounced.

The ratio P_{max}/living carbon (C), for all samples, showed maxima in April and August–September (Fig. 7), corresponding to the periods of rapid phytoplankton fresh weight biomass increase. The ratio did not differ significantly in the two Arms of the lake throughout the year. However, as with the assimilation numbers, there were often large differences in the P_{max}/C ratios with depth during the stratified season (Fig. 5 and Table 1).

Discussion

EXPERIMENTAL DESIGN

The frequent assumption, for productivity studies, of a homogeneous euphotic zone does not always apply for Kootenay Lake. Although late fall physical, chemical, and biological parameters suggest a mixed euphotic zone, this is certainly not the case during the rest of the growing season

when changes in phytoplankton biomass levels with depth are common (Fig. 8).

Because of heterogeneity it is necessary to monitor vertical variations in the photosynthetic characteristics of the phytoplankton. We determined two, and occasionally three, $P(I)$ curves for the euphotic zone. The use of chlorophyll measurements, which are relatively easy to obtain, was a further way of describing these vertical changes. The assumption here is, of course, that the potential photosynthesis at any depth is a direct function of phytoplankton chlorophyll. Our results did show a good correlation of P_{max} with chlorophyll a for data gathered from all the stations over the year ($r = 0.79$). However, because changes in species composition throughout the year probably affect this relationship, a better correlation would be expected for a particular set of data from one time and place. Indeed, data from specific monitors often showed higher correlations (e.g. August 11, $r = 0.97$, $n = 8$).

The determination of the inhibition part of the $P(I)$ curve also becomes important in a stratified euphotic zone. Inhibition, measured by fixed in-situ or constant light (incubator) incubations, may be overestimated if the natural populations are constantly mixed within the euphotic zone (Harris and Piccinin 1977; Marra 1978). In Kootenay Lake, however, surface heating during calm sunny weather often produces shallow transient thermal layers which tends to keep the surface-layer populations in a high light environment. During summer these populations often show daily volumetric productivities 40% lower than those at optimum depths. The result of this surface inhibition is to lower the daily euphotic zone integrals 10–15% from those integrals assuming optimum rates extrapolated to the surface. Although this inhibition effect on the integral is relatively small, considering all the errors involved in sample collection and measurement, a more important consequence is the change in the photosynthetic characteristics of the surface-layer populations. To measure these changes a bright light source in the incubator is essential.

The estimation of long-term areal productivities is accomplished by incorporating the continuous measurement of surface irradiance in the calculation procedure. This is a relatively simple task, requiring also that the parameters obtained on monitor dates be interpolated to estimate conditions during intervening days. Obviously, the shorter the time interval between monitors, the more accurate these estimated parameters become. Chlorophyll, for example, can be highly variable especially during times of rapid phytoplankton growth. Ideally, it would be desirable to have a more frequent sampling schedule for this parameter to supplement the more intensive studies necessary to obtain the $P(I)$ curves. Then all that is required is a minor modification to the computer routine to introduce this chlorophyll data, obtained between monitor dates, into the calculation of long-term areal productivities.

Areal Productivities and P_{max} Ratios

The annual value and range of areal productivities, in 1977, would characterize Kootenay Lake as mesotrophic (Wetzel 1975). The levels are similar to those from certain other large, deep, temperate lakes, e.g. Ontario (Stadelmann et al. 1974) and Michigan (Fee 1973a), but are substantially higher than those from two other large, deep, British Columbia lakes, Kamloops (St. John et al. 1976) and Babine (Stockner and Shortreed 1975). The range and mean daily productivities for the whole lake during the period May to September are similar to the same period measured in 1964 (Northcote 1973) and again in 1973–74 (R. N. Nordin and R. J. Crozier, B.C. Ministry of the Environment, Victoria, B.C., personal communication).

The assimilation number, P_{max}/chlorophyll a, of a phytoplankton community is dependent on many factors including temperature (Bothwell 1975; Eppley 1972), species composition and size distribution (Bothwell 1975), adaptation to light (Steeman-Nielsen et al. 1962), and degree of nutrient starvation (Glooschenko et al. 1974; Gächter et al. 1974). In Kootenay Lake the maximum assimilation numbers reflect the periods of more active phytoplankton accumulation (Fig. 7). This agrees with observations by Konopka and Brock (1978), who also found maximum assimilation numbers at the start of an increase in blue-green algal biomass and minimum numbers at the peak.

Normalizing P_{max} with respect to living carbon provides information about the carbon turnover rate (Vollenweider et al. 1974). The seasonal trends in Kootenay Lake (Fig. 7) generally parallel assimilation numbers with the occurrence of spring and fall maxima. In the case of P_{max}/C, however, the larger of the two annual peaks occurs in the spring. The carbon turnover rate at light saturation, 0.24 h^{-1}, at this time, is comparable to maximum rates in Lake Ontario (Vollenweider et al. 1974).

Riverine Effects

The measurement of lacustrine phytoplankton productivity can be complicated by river interflows. If the latter are sufficiently large they can dominate the physical and chemical properties of the lake and consequently influence the magnitude and distribution of primary productivity. Such is the case in several short residence-time lakes such as Koocanusa (Woods 1979), Kamloops (Carmack et al. 1979), and Powell (Gloss et al. 1980). In these lakes the rivers affect phytoplankton productivity through their influence on the euphotic zone and the epilimnion mixing depth. The result in these lakes is an overall reduction in lakewide productivity and a suppression of rates at locations close to the river inlets.

In Kootenay Lake, during 1964, a similar horizontal gradient in productivity was observed (Northcote 1973, unpublished data). High turbidities and flows associated with the Kootenay River during the spring freshet period resulted in a severe depression of rates in the extreme south end. The effect of the river, however, declined towards the middle of the lake as shown by increasing light penetration. Since 1964, upstream impoundments on both the Kootenay and Duncan rivers have resulted in changes in the river hydrographs. The springtime freshets have been greatly reduced and light penetration, particularly in the South Arm of the lake, has increased dramatically (Daley et al. 1981).

The effects of the rivers on phytoplankton productivity are now more subtle, as evidenced by the lack of a strong, hori-

zontal gradient in areal rates between stations. In fact, rather than showing suppressed rates, the extreme North and South Arm stations, close to the river inlets, sometimes show slightly higher values. Presumably, this is a result of proximity to the river nutrient supplies (Daley et al. 1981).

There is also evidence from our data that the rivers may affect the timing of the spring peak in productivity by influencing thermal stratification at that time of the year. The importance of stratification for initiating the spring peak is shown by reference to an earlier period. Several stations showed enhanced productivities and surface biomass levels in the late winter months (Fig. 4) when the lake surface was inversely stratified (e.g. surface temperature at N5 was 3.4°C on February 27). Productivity decreased in March, as surface temperatures warmed towards 4°C, and increased rapidly thereafter. The Kootenay River, entering as an overflow in March, aids in warming the surface layers of the South Arm and promotes stratification. However, the Duncan River flow at this time of the year is small and does not produce this effect, with the result that the spring peak in productivity occurs a few weeks earlier at S11 than at N5 (Fig. 4). It appears then, that instead of suppressing rates in the South Arm of the lake during the spring, the Kootenay River flows may now tend to enhance them.

Riverine processes in Kootenay Lake also influence vertical structure; indeed, the gradients of productivity parameters in the vertical are larger than those in the horizontal. Using the ratio P_{max}/C it is possible to view these gradients as changes in the photosynthetic characteristics of populations within the euphotic zone. Although differences in assimilation numbers with depth can reflect adaptation to different light regimes, the increases in P_{max}/C ratios with depth, with no discernible change in species composition, suggest that the deeper phytoplankton are less nutrient-deficient. Vertical differentiation has been identified in other lakes without strong riverine effects (Stadelmann et al. 1974). In Kootenay Lake, however, the interflows during summer and fall separate the euphotic zone from the nutrient-rich mesolimnetic and hypolimnetic waters. Carmack and Gray (1982) suggested that at this time the epilimnion is receiving nutrients primarily from these interflows. The phytoplankton vertical differentiation develops, in June to September, as transient shallow thermoclines prevent the euphotic zone from mixing completely. Consequently, frequent breakdown of these thermoclines and mixing of the deeper phytoplankton populations and nutrients into the surface layers could be an important process in enhancing summer and fall productivities.

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Particle-Size-Conversion Efficiency and Contaminant Concentrations in Lake Ontario Biota

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BORGMANN, U., AND D. M. WHITTLE. 1983. Particle-size-conversion efficiency and contaminant concentrations in Lake Ontario Biota. Can. J. Fish. Aquat. Sci. 40: 328–336.

The particle-size-conversion efficiency (log food consumption/production divided by log predator prey size ratio) is shown to be directly related to the relationship between the concentration of persistent contaminants accumulated primarily through the food chain and body size for organisms in pelagic ecosystems. The difference between particle-size-conversion efficiency for biomass and that for the contaminant gives the slope of the relationship between log contaminant concentration and log body size. This provides a useful theoretical framework for analyzing contaminant concentrations in aquatic biota without the need for specifying trophic level but still incorporating the idea of food chain accumulation. Concentrations of PCB, DDT, and mercury were examined in aquatic organisms from Lake Ontario, ranging in size from zooplankton to large salmonids (a 10^8-fold range in dry weight). The slope of the double log plot of concentration versus weight varied from 0.20 to 0.22 for PCB and DDT and was approximately equal to 0.13 for mercury. This indicates that mercury is accumulated less efficiently through the food chain than PCB or DDT. After correcting for incomplete uptake and retention of the contaminant, an estimate of particle-size-conversion efficiency for biomass of about 0.26 was obtained, which agrees reasonably well with previous estimates obtained from growth efficiency experiments and analysis of particle-size spectra. These calculations indicate that potential fish production in Lake Ontario is ~120-fold lower than zooplankton production (for fish averaging 10^8-fold larger in body size as compared to zooplankton).

Key words: particle-size-conversion efficiency, PCB, DDT, mercury, zooplankton production, fish production

BORGMANN, U., AND D. M. WHITTLE. 1983. Particle-size-conversion efficiency and contaminant concentrations in Lake Ontario Biota. Can. J. Fish. Aquat. Sci. 40: 328–336.

Le rendement de conversion par grosseur de particules (log consommation alimentaire/production divisé par log rapport de taille prédateur/proie) est en relation directe avec le rapport entre la concentration des contaminants persistants accumulés surtout dans la chaîne alimentaire et la grosseur du corps des organismes d'écosystèmes pélagiques. La pente de la relation entre le log de la concentration des contaminants et le log de la grosseur du corps s'obtient par différence entre le rendement de conversion par taille des particules de la biomasse, d'une part, et le contaminant, d'autre part. Ceci permet d'analyser la concentration des contaminants dans les biocénoses aquatiques, sans qu'il soit nécessaire de spécifier le niveau trophique, tout en incorporant l'idée d'une accumulation dans la chaîne alimentaire. Nous avons mesuré les concentrations de BPC, de DDT et de mercure dans des organismes aquatiques du lac Ontario, dont la taille variait de celle du zooplancton à celle des grands salmonidés (une gamme de 10^8 en poids sec). La pente du double tracé logarithmique de la concentration versus le poids varie de 0,20 à 0,22 pour les BPC et le DDT, et est à peu près égale à 0,13 pour le mercure. Ceci indique que ce dernier s'accumule moins efficacement que les BPC ou le DDT dans la chaîne alimentaire. Après avoir appliqué une correction pour tenir compte d'une absorption et d'une rétention incomplètes du contaminant, nous avons obtenu une estimation du rendement de conversion par taille de particules d'environ 0,26 pour la biomasse. Ceci s'accorde assez bien avec des estimations antérieures découlant d'expériences sur l'efficacité de la croissance et d'une analyse des spectres de taille des particules. D'après ces calculs, la production potentielle de poisson dans le lac Ontario est environ 120 fois

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moindre que celle du zooplancton (pour des poissons dont la taille est en moyenne de 10^x fois celle du zooplancton).

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MODELING of biomass or energy flow in aquatic ecosystems has always been a difficult task, especially when attempts are made to use easily measured quantities in the models. For pelagic systems, where trophic level is largely a function of the organism's size, the mathematics of relating production at different trophic levels has been greatly simplified by the introduction of the concept of particle-size-conversion efficiency; this is a measure of efficiency of conversion of biomass from one size to another, rather than from one trophic level to another (Borgmann 1982). This concept permits direct analysis of data on biomass and production rates for different-sized organisms, without the necessity of identifying trophic levels. The major drawback with this concept is the present lack of estimates of particle-size-conversion efficiencies under natural conditions. This problem also exists for conventional conversion efficiencies (K_1 = biomass production per food consumption). Although much information is available on K_1 for fish fed artificial diets, very little data have been collected on efficiency under natural conditions where fish must actively forage for their food. However, Niimi (1981) has shown that a considerable insight into conversion efficiencies in nature can be obtained from concentrations of persistent contaminants in organisms and their food. In this paper we will show that the relationship between contaminant concentration and body size (dry weight) of species at different trophic levels is directly related to the particle-size-conversion efficiency. Consequently, it is possible to estimate particle-size-conversion efficiency in a multitrophic level ecosystem from contaminant concentrations in the biota.

For several years the concentrations of contaminants in a wide variety of Lake Ontario biota have been determined for the surveillance program of the Great Lakes Fisheries Research Branch. This data set provides an opportunity to test and demonstrate the application of the particle-size-conversion efficiency concept, both with respect to providing a simple theoretical framework for analysis of contaminants data, and for providing an actual estimate of particle-size-conversion efficiency for a specific ecosystem. These calculations are directly relevant to the estimation of both contaminant bioaccumulation through the food chain and the potential fish production in Lake Ontario. They also demonstrate that analysis of a complex ecosystem does not require complex mathematics, and that simple relationships such as that between contaminant concentration and body size are sometimes all that are needed to obtain some understanding of how the ecosystem functions.

Theory

The relationship between contaminant concentration and body size in aquatic organisms in a pelagic ecosystem can be related to the particle-size-conversion efficiency. Particle-size-conversion efficiency (for biomass) in a single link in the food chain is given by (Borgmann 1982)

$$(1)\quad \epsilon = \frac{-\log K_1}{\log W_j/W_i} = \frac{\log C/P}{\log W_j/W_i}$$

where ϵ is a measure of particle-size-conversion efficiency, C is the food consumed per unit time by the predator, P is biomass production by the predator over the same time interval, and K_1 is the conventional definition of conversion efficiency (i.e. P/C). W_j and W_i are the size of the predator and prey, respectively. Log K_1 in equation 1 is multiplied by -1 to make ϵ positive in most situations encountered in pelagic environments where W_j/W_i is greater than 1. Whereas K_1 is a measure of the efficiency of conversion of biomass from one trophic level to the next, ϵ is a measure of the efficiency of conversion of biomass from one size to another. If amount of prey consumed and predator production are plotted against prey and predator size, respectively, a line of slope $-\epsilon$ is obtained. A high K_1 results in a low ϵ and vice versa. Borgmann (1982) demonstrated that for various published data on carnivorous zooplankton and fish, ϵ was at least as constant as K_1 (we have not yet attempted similar calculations for herbivores). This suggested that efficiency of biomass transfer up a food chain is largely a function of the sizes of the organisms at the bottom and top of the food chain, and independent of the number of trophic levels. Consequently, potential fish production can be estimated more readily from a knowledge of ϵ than from K_1, as the number of trophic levels in the food chain need not be determined.

It is possible to use the particle-size-conversion efficiency concept to simplify analysis of data on contaminant concentrations at different trophic levels, for those compounds accumulated primarily through the food chain. This can be done by defining particle-size-conversion efficiency for the contaminant (ϵ'), analogous to the definition for ϵ based on biomass.

$$(2)\quad \epsilon' = \frac{\log C'/P'}{\log W_j/W_i}.$$

Equation 2 is equivalent to equation 1, except that the food biomass consumed (C) has been replaced with the amount of contaminant consumed in the diet (C') and the biomass production (P = biomass retained and not excreted or metabolized) is replaced by the amount of contaminant retained and not excreted or metabolized (P'). If the amount of contaminant consumed and the amount retained are plotted against prey and predator size, respectively, a line of slope $-\epsilon'$ is obtained. ϵ' is a measure of the efficiency with which the contaminant is retained from one size organism to another, rather than from one trophic level to another. Similar to the case of ϵ, a high retention of contaminant results in a low ϵ' and vice versa. If all the contaminant in the food is absorbed and retained, C'/P' equals 1.0 and ϵ' equals 0. Both ϵ and ϵ' are dimentionless quantities, and the units used to measure C, P, C', P', W_j, and W_i are irrelevant as long as they are

consistent (i.e. all biomass units are grams dry weight or calories, and all contaminant units are grams or moles, etc.).

Equation 2 is a valuable expression of contaminant transfer up the food chain because it can be combined with equation 1 to give a simple equation relating body size to contaminant concentration. The concentration of the contaminant in the food is given by C'/C and the concentration of the contaminant resulting in the predator after a steady state is reached is given by P'/P. Consequently, the ratio of contaminant concentration in the predator divided by that in the prey is given by

$$(3) \quad \frac{P'/P}{C'/C} = \frac{C/P}{C'/P'} = \left(\frac{W_j}{W_i}\right)^{\epsilon - \epsilon'}.$$

Taking the logarithm of equation 3 and rearranging the equation gives

$$(4) \quad \log (P'/P) = (\epsilon - \epsilon')\log W_j + [\log (C'/C) - (\epsilon - \epsilon') \times \log W_i].$$

Previous analysis of the published literature has suggested that it is reasonable to assume that ϵ is relatively constant when modeling biomass flow through pelagic ecosystems (Borgmann 1982). Consequently, $\epsilon - \epsilon'$ in equation 4 can be assumed to be roughly constant for those contaminants which were retained efficiently within the body (i.e. low ϵ', therefore $\epsilon \gg \epsilon'$). A plot of the logarithm of contaminant concentration (P'/P) against log body size should therefore give a straight line of slope $\epsilon - \epsilon'$ (equation 4). By repeating the above calculation for the next trophic level (i.e. replacing W_i by W_j and W_j by its predator, etc.) it can be shown that P'/P in equation 4 can be replaced by contaminant concentration at any trophic level and W_j with body size at that trophic level without changing the expression inside the square brackets. For a contaminant which is assimilated and retained with 100% efficiency, $\epsilon' = 0$, and the slope of the contaminant concentration versus body size plot is equal to ϵ. For contaminants accumulated at less than 100% efficiency, the slope will be less. Consequently, it is possible either to predict contaminant concentrations at other levels in the food chain from a knowledge of ϵ and contaminant concentrations at one trophic level, or to estimate the value of ϵ (or at least its minimum value) from a knowledge of contaminant concentrations at several trophic levels. Such calculations are, of course, only meaningful for contaminants that are accumulated primarily from the food, rather than the water.

The above analytical technique is designed for examining contaminant concentrations among different trophic levels, and not for describing the concentration versus size relationship within a single species. For many fish species, growth, and therefore growth efficiency, decrease with age. Populations of such fish may contain a few large individuals which contribute a minimal amount to total production and, because of their low growth efficiency, have accumulated high contaminant levels. Consequently, the slope of the contaminant concentration versus body size plot for a single species is a function of physiological changes during the life cycle of the organism, and not an indication of the average particle-size-conversion efficiency within the ecosystem. However, data on contaminant concentrations for single species can be used to estimate changes in conversion efficiency with organism age (e.g. Niimi 1981), although this will not be attempted here.

Materials and Methods

Collections of zooplankton, *Pontoporeia affinis* (a benthic amphipod), mysids (*Mysis relicta*), slimy sculpins (*Cottus cognatus*), rainbow smelt (*Osmerus mordax*), lake trout (*Salvelinus namaycush*), and coho salmon (*Oncorhynchus kisutch*) were made in the eastern and western basins of Lake Ontario. Collection locations for the eastern region included offshore sites near Big Bar Shoal (44°05′N; 76°40′W), Main Duck Island (43°55′N; 76°35′W), and Point Traverse (43°50′N; 76°50′W). Collection sites in the western region included areas near Port Credit (43°30′N; 79°35′W) and Port Dalhousie (43°20′N; 79°05′W). Coho salmon in the western region were collected during the spawning run on the Credit River near Streetsville (43°35′N; 79°45′W). Samples were collected between August and October, although invertebrate, sculpin, and smelt samples in the eastern region were also collected from April to November in 1977 and 1978. Data presented here are for 1977, 1978, and 1979. Collections were made with the cooperation of the Ontario Ministry of Natural Resources, Fisheries Branch, as part of the International Joint Commission, Great Lakes International Fish Contaminants Surveillance Program.

Samples of net plankton were collected using Wisconsin type nets (0.5 × 1.5 m; 153 μm mesh) towed horizontally at a depth of 1 m. During all tows, contamination from the boat's wake and surface slicks was avoided. Collections of *Pontoporeia* and *Mysis* were made with an epibenthic sled (Elster 1933). *Pontoporeia* were held at 4°C for 12 h to allow their gut content to clear. All collection gear was constructed of steel and aluminum framing with nylon netting. All collections were made during the day and samples were initially held at 4°C in acid-washed and acetone–hexane rinsed glassware. They were then dried at 60°C for 24 h, ground in a glass mortar with pestle, and subdivided into a minimum of five aliquots per sample. All processing equipment was washed and rinsed in distilled water, acetone, and hexane between each sample. All samples were stored in acid-washed and solvent-rinsed glass containers until analysis.

Slimy sculpins were collected with the epibenthic sled at depths from 20 to 30 m. Other fish species were collected by overnight bottom sets of monofilament gill nets ranging in size from 3.8- to 15.2-cm stretched mesh. After collection, whole fish were wrapped in hexane-rinsed aluminum foil and stored at −25°C until homogenization. Samples of sculpins and smelt were processed as composites of five similar-sized fish whereas the remaining fish were treated individually. Fish were weighed, measured, and sexed and then homogenized a minimum of five times with a commercial meat grinder. All equipment and processing instruments were washed between each sample, rinsed in distilled water, acetone, and hexane. Aliquots of 50 g of the whole fish homogenates were stored in acid-washed and acetone–hexane rinsed glass containers at −25°C until trace metal and pesticide residue analyses were performed.

TABLE 1. Overall mean size and contaminant concentrations (dry weight basis) for organisms from the eastern basin of Lake Ontario (1977–79). All values are logarithmic means. Concentrations in fish are calculated assuming a 75% moisture content. For invertebrates, n = total number of separate samples collected (most samples were subdivided into four replicates for contaminant analysis). For fish, n = total number of fish analyzed over the 3-yr period.

Organism	Body Weight (g)	PCB (μg/g)	DDT (μg/g)	Mercury (μg/g)	n
Zooplankton	2×10^{-6}	0.20	0.06	0.06[a]	20
Pontoporeia	1.34×10^{-3}	1.70	0.69	0.11[b]	8
Mysis	5.31×10^{-3}	0.29	0.12	0.10[c]	12
Sculpin	0.659	3.82	0.97	0.71	53
Smelt	4.22	2.38	0.78	0.21	109
Lake trout	246	14.1	4.92	0.64	216

[a] $n = 15$.
[b] $n = 3$.
[c] $n = 9$.

Pontoporeia and sculpins are benthic organisms, rather than pelagic (for which the particle-size-conversion efficiency concept was first developed), but are included because sculpins are an important food source for lake trout and *Pontoporeia* are the principal food for sculpins. Data were not collected on sculpins in western Lake Ontario. Data on coho salmon, on the other hand, are available only for the western basin of Lake Ontario. Coho were not available in the eastern region during the years sampled.

PCB and DDT analyses were performed by the Ontario Ministry of Agriculture and Food, Provincial Pesticide Residue Testing Laboratory, using gas chromatography with a Ni^{63} electron capture detector as described by Frank et al. (1978). DDT residues are given as total DDT, including *p*, *p*′-DDE, *p*,*p*′-TDE (DDD), *p*,*p*′-DDT, and *o*,*p*′-DDT. Mercury analyses were performed by Water Quality Branch, Inland Waters Directorate, using cold vapor atomic absorption spectrometry as outlined in the Department of Environmental Analytical Methods Manual (1979).

Data Analysis

Double log regressions were performed separately for PCB, total DDT, and mercury concentrations, on a dry weight basis, against organism dry weight, for both the eastern and western basins of Lake Ontario. Each data point used in the interspecies regression was a logarithmic mean of contaminant concentration and body size for all data collected at one site for 1 yr. For the fish, these points were obtained from double log regressions of individual fish contaminant levels versus body weight for each site. Contaminant concentrations in fish were measured on a whole fish wet weight basis and converted to dry weight assuming a water content of 75%. Dry weight measurements were made for only sculpins and some smelt, and these provided estimates of water content of 75.7 and 75.6%, respectively. Mean length measurements were made on some of the *Mysis* and *Pontoporeia*, and these were converted to dry weight using the length–weight relationships of Lasenby and Langford (1972) for *Mysis* from Stony Lake, Ont., and of Ron Dermott (Great Lakes Fisheries Research Branch, Burlington, Ont., personal communication) for *Pontoporeia* from Lake Ontario. Zooplankton counts indicated that the dominant organisms present were always either cyclopoid copepodites or *Bosmina longirostris*, each of which have an average dry weight of roughly 2 μg (unpublished data).

In addition to the above regressions, the relationship between total lipid concentrations and PCB and DDT levels were also examined. Double log regressions were performed on individual fish PCB and DDT concentrations, expressed per unit lipid, versus body size, for each site, for each year. Means of these values were then used in interspecies regressions, just as done for concentration on a dry weight basis.

Results

Contaminant concentrations in Lake Ontario biota are summarized in Tables 1 and 2 and Fig. 1 and 2. The slopes for the regression lines for contaminant concentrations versus body size (dry weight), summarized in Table 3, are all significantly positive at $P < 0.001$. There is no doubt, therefore, that contaminant concentrations are higher at higher trophic levels. The slopes (Table 3) are estimates of $\epsilon - \epsilon'$, averaged over several trophic levels. For both PCB and DDT these are equal to ~0.22 for the eastern and 0.20 for the western basin of Lake Ontario (Fig. 1 and 2). The slopes for mercury for each basin, however, are lower and approximately equal to 0.13. Consequently, ϵ' for mercury is higher than for PCB or DDT.

The validity of the above analysis is dependent on the assumption that contaminants are accumulated primarily from the food, and not the water. The accuracy of this assumption was tested by examining contaminant concentrations on a lipid basis. If contaminants are accumulated from water and are more or less in equilibria with water levels, then it would be expected that PCB and DDT concentrations would be related to lipid levels, because these contaminants dissolve preferentially in lipids. Consequently, if PCB and DDT concentrations on a lipid basis show no relationship to body size, the possibility of water uptake cannot be excluded. Such a situation is in fact observed in lake trout. The average slopes

TABLE 2. Overall mean size and contaminant concentrations (dry weight basis) for organisms from the western portion of Lake Ontario (1977–79). All values are logarithmic means. Concentrations in fish are calculated assuming a 75% moisture content. n = number of samples collected as in Table 1.

Organism	Body Weight (g)	PCB (μg/g)	DDT (μg/g)	Mercury (μg/g)	n
Zooplankton	2×10^{-6}	0.31	0.08	0.04[a]	4
Pontoporeia	1.34×10^{-3}	1.67	0.48	—[b]	4
Mysis	5.31×10^{-3}	0.39	0.28	0.12	4
Smelt	6.90	6.75	2.20	0.36	50
Lake trout	177	20.7	5.70	0.69	110
Coho salmon	434	9.14	3.26	0.44	206

[a]n = 2.
[b]Not available.

TABLE 3. Slope and 95% confidence limits of the regression line between log contaminant concentration and log body weight for all species combined from eastern and western Lake Ontario (Fig. 1–4). All values based on dry weights (assuming 75% moisture content in fish).

Contaminant	Slope for eastern basin	Slope for western basin
PCB	0.217±0.050	0.203±0.042
DDT	0.222±0.047	0.206±0.040
Mercury	0.129±0.032	0.136±0.023

of the double log regression of PCB and DDT per unit dry weight are 0.411 and 0.496, respectively (Table 4), but these drop to −0.065 and 0.023, respectively, when PCB and DDT concentration are decribed on a lipid basis. This is due to the large increase in lipid content with body size in lake trout, making it impossible to demonstrate whether contaminant levels are related primarily to body size or to lipid content. For smelt, on the other hand, the situation is entirely different. The average slopes for PCB and DDT concentrations on a dry weight basis are 0.812 and 0.710, respectively (Table 4). When expressed as PCB or DDT per unit lipid, the slopes average 0.704 and 0.602, respectively, indicating a strong size dependence, even on a lipid basis. For the single regression lines, 7 out of 10 for PCB and 4 out of 10 for DDT are significant at $P < 0.05$, on a dry weight basis, whereas 6 out of 10 for PCB and 4 out of 10 for DDT are still significant on a lipid basis. Some slopes are not significant due to the small size range of fish sampled at a given site at a given period. For smelt, therefore, contaminant concentrations are not related simply to lipid content, as expected if water uptake predominated over food uptake. Coho collected from the Streetsville site present a picture similar to that of smelt, whereas those collected near Port Dalhousie contain too small a size variation to provide significant slopes. Sculpins demonstrate little size effect on contaminant levels, either on a dry weight or on a lipid basis, due partly to the small size range of organisms collected. Overall, the smelt and coho data suggest that PCB and DDT levels are not related to total lipid concentration, and the positive correlation in lake trout is therefore probably spurious. Regressions of PCB and DDT on a lipid basis were also done for the interspecies comparisons, as in Fig. 1 and 2. Although the slopes are slightly lower on a lipid basis (0.18 in the western and 0.14 in the eastern basis for both PCB and DDT), they are all significant at $P < 0.001$, again indicating that contaminant concentrations are not controlled by fat levels in these organisms.

Although body size and contaminant concentration are related and although this is not controlled by lipid levels, not all species in Fig. 1 and 2 fit exactly on the regression line. In particular, *Pontoporeia* have usually high PCB and DDT concentrations, relative to their size. This is probably due to their benthic existence. If the sedimenting material on which they feed has a lower nutritional value than that consumed by the other invertebrates, and if it contains similar amounts of sorbed contaminants, *Pontoporeia* would have to injest larger amounts of PCB and DDT to achieve the same amount of growth as pelagic invertebrates. Their higher contaminant levels would then be passed on to sculpins, which also have higher PCB and DDT levels relative to their size than, for example, smelt. Lake trout have higher contaminant levels than coho salmon, possibly because they feed in part on sculpins, but also because they are older, slower-growing fish, relative to coho, and therefore probably have a lower growth efficiency.

Another species not quite on the regression line is *M. relicta*. These organisms have a consistently low PCB and DDT concentration, relative to their body size. In fact, a linear regression of only mysid and zooplankton data for PCB and DDT never gives a positive slope significant at $P < 0.05$, either on a dry weight or a lipid basis. The mercury concentrations for zooplankton and mysids, on the other hand, are significantly related to size at $P < 0.05$ in the eastern and $P < 0.01$ in the western basin of the lake. Two possible explanations for these observations can be given. The first is based on the collection procedure. About 24 h had elapsed before the mysids were sorted from the other debris following collection. Although mysids were stored at 4°C during this time, surface slicks of oil were visible, indicating some loss of body lipid from these fairly fragile organisms. Recent experiments have indicated that 40% of the body lipid can be lost in 24 h, and 60% in 48 h. If the PCB and DDT loss is proportional to lipid loss, true concentrations for these organic contaminants in fresh mysids might have been about twice as high as indicated in Fig. 1 and 2. This would bring the mysid data points much closer to the regression line. Loss of mercury would theoretically be less, as it is not associated as strongly with lipid, and hence the uncorrected mercury data fits

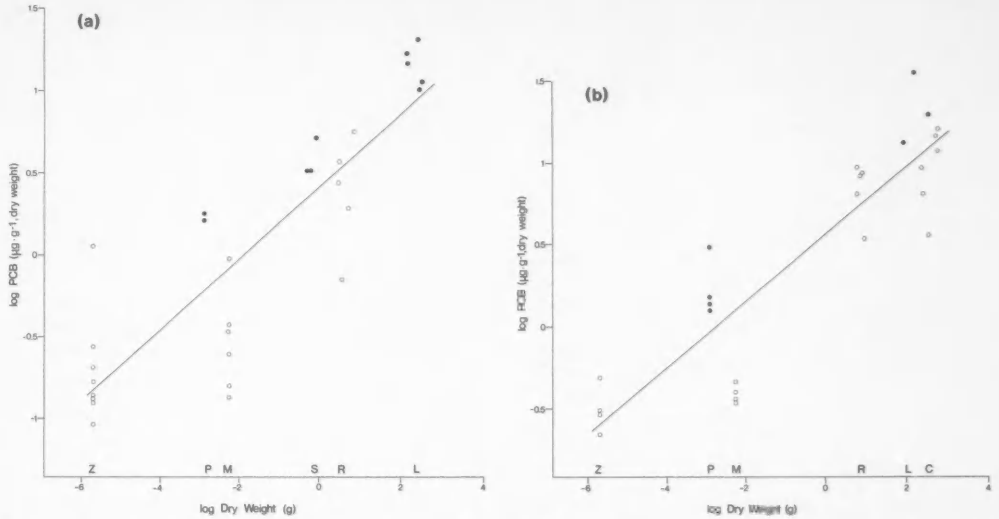

FIG. 1. PCB concentration as a function of body size in aquatic organisms from (a) the eastern portion and (b) the western portion of Lake Ontario. Each point represents the yearly logarithmic mean for one collection site for 1977, 1978, or 1979. Z, zooplankton; P, *Pontoporeia affinis*; M, *Mysis relicta*; S, slimy sculpin; R, rainbow smelt; L, lake trout; C, coho salmon.

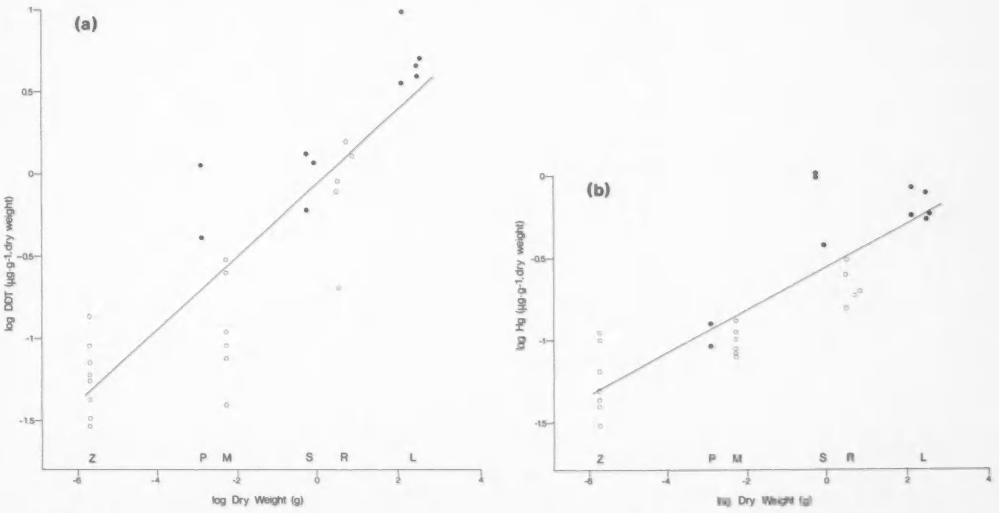

FIG. 2. (a) DDT concentrations and (b) mercury concentrations as a function of body size in aquatic organisms from the eastern portion of Lake Ontario. Symbols as in Fig. 1.

closer to the regression line (Fig. 2, Tables 1 and 2). A second possible explanation is that PCB and DDT are not related to body size or trophic level for zooplankton and mysids, because of their small size and consequent large body surface to volume ratio and high metabolic rate. Their body concentrations of organic contaminants might be related more closely to water levels, as found, for example, by Clayton et al. (1977) for marine zooplankton.

Discussion

The data in Fig. 1 and 2 are unique, because they give

TABLE 4. Mean of the slope of the regression line between log contaminant concentration and log body size within individual species of fish.

Fish	Mean slope for: PCB	DDT	mercury
Sculpin	0.185	0.177	−0.790
Smelt	0.812	0.710	0.258
Lake trout	0.411	0.496	0.281
Coho salmon	0.445	0.325	0.285

contaminant concentrations as measured over several years, in the same ecosystem, over a large organism size range, and with organisms collected and analyzed in the same laboratory and using the same analytical technique. The results demonstrate a definite relationship between organism size and PCB, DDT, and mercury concentrations. Other researchers have also indicated a relationship between organism size and contaminant concentrations (e.g. Thomann 1981) but have usually done so utilizing published data from a wide variety of sources representing several different ecosystems. The extent of our data for the Lake Ontario pelagic ecosystem makes it possible to estimate average values of the difference between particle-size-conversion efficiency for biomass and for PCB, DDT, and mercury ($\epsilon - \epsilon'$) within this system. For PCB and DDT, $\epsilon - \epsilon'$ is about 0.20–0.22, when all organisms are included. The value of $\epsilon - \epsilon'$ for mercury is about 0.13 (Table 3). The importance of including the benthic organisms (*Pontoporeia* and sculpins) in these calculations is not certain. However, their omission has a negligible effect on the estimate of $\epsilon - \epsilon'$ in the eastern basin of the lake and raises the estimate of $\epsilon - \epsilon'$ to only 0.216 for PCB and 0.215 for DDT in the western basin. Consequently, whether or not benthic and pelagic food chains are combined does not seriously affect estimates of $\epsilon - \epsilon'$.

Woodwell et al. (1967) measured DDT residues in a wide range of organisms from a salt marsh and observed increasing DDT concentrations with increasing size and trophic level, although they did not give actual sizes of the animals they measured. Griesbach et al. (1982) estimated sizes for the aquatic organisms studied by Woodwell et al. (1967) and plotted log DDT concentrations against log body size. Extrapolation off this graph gives an estimated slope of about 0.23, which is close to our slopes for DDT concentration in Lake Ontario biota, in spite of the fact that one system is pelagic and the other a marsh habitat. Similarly, the log–log plot of the concentration factor for PCB against organism size for data from many sources appears to give a slope of roughly 0.2, as extrapolated off the figure given by Thomann (1981). Consequently, it is possible that $\epsilon - \epsilon'$ may be relatively uniform for PCB and DDT in a wide variety of aquatic habitats, not just pelagic ecosystems.

One comparison of our data with published values from Lake Ontario is possible. Norstrom et al. (1978) reported concentrations of several contaminants in coho salmon and in their stomach contents, consisting of alewives (*Alosa pseudoharengus*) and smelt. The ratio of PCB concentrations in salmon muscle to prey items was 2.6, and the mean ratio for all contaminants was 2.9. From the mean size of the salmon (2393 g wet weight) and the average of the alewife and smelt sizes (14.4 g), a value of $\epsilon - \epsilon'$ of 0.208 can be calculated (using the mean concentration ratio for all contaminants). This value is almost identical with our estimates of $\epsilon - \epsilon'$ in the western end of Lake Ontario (Table 3). The ratio of contaminant concentration in coho to that in smelt from our data is 1.35 for PCB and 1.48 for DDT (Table 2), considerably lower than the mean ratio obtained by Norstrom et al. This, however, is due to the fact that our mean smelt size is larger (27.6 g wet weight) and our mean coho size smaller (1736 g) than the fish sizes examined by Norstrom et al. If we correct our contaminant concentrations to fish sizes equivalent to those of Norstrom et al., using our observed relationship between contaminant concentration and fish size for each species (Table 4), we obtain contaminant ratios in coho to smelt of 2.65 for PCB and 2.61 for DDT, which are similar to the ratios obtained by Norstrom et al. These calculations demonstrate the need for determining accurately predator and prey size, and contaminant concentrations at the correct size, before attempting to calculate conversion efficiencies for single trophic steps from contaminant data.

It is now possible to estimate particle-size-conversion efficiency for biomass (ϵ) in the Lake Ontario ecosystem. This requires an estimate of ϵ'. The resultant estimate of ϵ is likely to be most acurate when using contaminants for which ϵ' is smallest, because a relative error in the estimation of ϵ' will then have the smallest possible effect on the estimate of ϵ. PCB and DDT appear to have similar ϵ' values, which are lower than ϵ' for mercury (i.e. because $\epsilon - \epsilon'$ is larger). A reasonable estimate of ϵ' for PCB and DDT would probably be about 0.05. This is equivalent to a retention of PCB or DDT (P'/C', equation 2) of 79% for a predator prey size ratio of 100 and 50% for a predator prey size ratio of 10^6. At intermediate predatory prey size ratios of 10^3, 10^4, and 10^5, this is equivalent to retention efficiencies of 71, 63, and 56%, respectively. Experimental estimates of the amount of PCB or DDT retained from the diet are rare. Lieb et al. (1974) calculated a 68% retention of PCB from the diet of rainbow trout, and Roberts et al. (1977) indicated that in preliminary experiments greater than 80% of the ingested dose of DDT was assimilated by brown bullheads (*Ictalurus nebulosus*). Guiney and Peterson (1980) observed 70–80% retention of tetrachlorobiphenyl in yellow perch (*Perca flavescens*) and rainbow trout (*Salmo gairdneri*). Warlen et al. (1977) in studies on menhaden, a planktivorous fish with a high predator prey size ratio, calculated that 17–27% of the DDT offered was retained. However, not all the food was eaten and actual assimilation of ingested DDT could have been greater by 20% or more. Cox (1971) estimated that 62 and 76% of DDT in food was assimilated by euphausiid shrimp in separate experiments. Therefore 0.05 appears to be a reasonable estimate for ϵ'. This indicates then that ϵ in the Lake Ontario ecosystem studied has a value of about 0.25–0.27. Note that a large relative error in estimating ϵ' would result in only a small relative error in the estimate of ϵ, because ϵ is much greater than ϵ'. Our estimate of ϵ is larger than previous estimates of particle-size-conversion efficiency estimated from laboratory studies on growth efficiency of zooplankton and from feeding and growth of walleye (*Stizostedion vitreum vitreum*) ($\epsilon = 0.21$). It is close, however, to the estimate of

$\epsilon = 0.24$ for a marine ecosystem obtained from the data of Sheldon et al. (1977) on the particle-size spectrum and the relationship between growth rates and organism size (Borgmann 1982). It will be of interest to compare our estimate of particle-size-conversion efficiency, obtained for a relatively mesotrophic freshwater ecosystem, with further estimates from other pelagic environments when these data become available. It is possible that ϵ may be relatively uniform in many ecosystems, as indicated above by the similarity in $\epsilon - \epsilon'$ for PCB and DDT from diverse data sets.

Our analysis shows that the use of the particle-size-conversion efficiency concept (equations 1 and 2) provides an unusually simple theoretical framework for interpreting contaminant concentration data in pelagic ecosystems. This is similar to the simplification obtained using this concept when studying whole community production, biomass transfer up the food chain, and the shape of the biomass size spectrum (Borgmann 1982). By describing conversion efficiency on a size-corrected basis, it is possible to obtain estimates of an important ecological parameter (i.e. $\epsilon - \epsilon'$) simply by plotting contaminant concentration against organism size. Other models of contaminant transfer up the food chain (e.g. Thomann 1981) consider contaminant uptake kinetics from both water and food in much more detail, and such models are doubtless of considerable value in studying the mechanisms of contaminant dynamics. However, the considerable mathematics involved in many such models discourages less mathematically inclined researchers from examining their data in a more theoretical framework. The concept of particle-size-conversion efficiency, on the other hand, provides a simple theoretical basis for interpreting contaminant data which can be used with a minimum of mathematics.

The difficulty in identifying food chains or webs accurately in nature, and the resultant problems in modeling contaminant concentrations, has prompted some researchers to develop models that ignore food chain accumulation entirely, and rely only on various allometric relationships. Although such models are valuable in demonstrating the temporal changes in contaminant concentrations at different trophic levels after addition of a contaminant pulse (e.g. Griesbach et al. 1982), contaminant concentrations under steady state conditions are not necessarily modeled accurately. For example, if elimination of a contaminant is proportional to body metabolism, and if contaminant uptake is proportional to food intake which is in turn proportional to metabolism, contaminant concentrations at steady state would be independent of body size (Fagerström 1977). In reality, larger organisms would be expected to have higher concentrations of contaminants such as PCB and DDT, if contaminant elimination is proportional to whole body metabolism, because contaminant concentrations in food are greater for larger organisms. For accurate modeling of such contaminants, food chain accumulation must be taken into account, and this is done in our model without the need for specifically identifying trophic levels.

In addition to providing insights into contaminant dynamics in Lake Ontario, our analysis also provides another much needed and independent estimate of the particle-size-conversion efficiency for biomass (i.e. $\epsilon \sim 0.26$). This, in turn, makes it possible to estimate potential fish production from production of forage fish or zooplankton using simple equations modified after Borgmann (1982) such as

$$(5) \quad P_f = P_z(W_z/W_f)^{\epsilon}$$

where P_f is fish production, P_z is zooplankton production, and W_z and W_f are zooplankton and fish sizes, respectively (on a dry weight basis). Equation 5 can be obtained from equation 1 by replacing W_j with W_f, W_i with W_z, P with P_f, and C with P_z. This assumes that net zooplankton production (P_z) is equal to fish consumption (C) at steady state. Although equation 1 applies to a single step in the food chain, it can readily be shown (Borgmann 1982) that equation 5 applies to any number of steps in the food chain if ϵ is approximately constant. Zooplankton production rates in Lake Ontario have recently been estimated (H. Shear, Great Lakes Fisheries Research Branch, Burlington, Ont., personal communication). For the six stations studied throughout the lake, the preliminary estimate of mean biomass production in the epilimnion is 1.8 $g \cdot m^{-3} \cdot yr^{-1}$. Assuming an approximate epilimnion depth of 10 m, this gives a production of 18.0 $g \cdot m^{-2} \cdot yr^{-1}$ (dry weight basis). If we now assume a 10^8-fold average size increase from zooplankton to fish (i.e., from 2×10^{-6} g dry weight for zooplankton to 200 g dry weight or 800 g wet weight for fish, Fig. 1 and 2), this gives a value of $(W_z/W_f)^{\epsilon}$ in equation 5 of about 1/120. Consequently potential fish production in Lake Ontario could be about 18.0/120 or 0.15 $g \cdot m^{-2} \cdot yr^{-1}$. This compared with a maximum commercial fish production in the past for Lake Ontario of roughly $4\frac{1}{2}$ million pounds (2×10^6 kg) per year (Rawson 1952; Christie 1972), or about 0.025 $g \cdot m^{-2} \cdot yr^{-1}$ (dry weight, assuming a 75% water content for fish). Consequently, an increase over past years in commercial fish production may be possible, if a balanced species composition and abundance can be maintained.

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Effort Dynamics of the Northern California Dungeness Crab (*Cancer magister*) Fishery

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Knowledge of the dynamic response of fishing effort to abundance is essential to a complete understanding of the cycles in catch in the northern California Dungeness crab fishery. In this fishery there is a lagged response of harvest rate to changes in abundance that is caused either by a time lag in fishermen entering and leaving the fishery following changes in abundance, a lag in market expansion and contraction following changes in abundance, or a combination of both. The time lag in this response appears to have decreased over the past 30 yr. This lagged response is a potential cause of the cycles. However, neither of the two potential cyclic mechanisms examined here, a predator–prey mechanism (with man as the predator) and a price-dependent escapement mechanism (with price dependent on past catch), is a cause of these cycles. Although time-varying effort does not cause the cycles, it does have a substantial effect on the resulting catch record and population dynamics. If there is a density-dependent recruitment mechanism in this population as proposed earlier, the presence of this lagged response would cause the period of observed cycles to be longer than would be expected on the basis of population dynamics alone. Hence, previous estimates of the expected period of cycles from various population mechanisms are low. Removal of this response is a potential means of stabilizing this fishery.

Key words: effort, Dungeness crab, harvest rate, predator–prey, price, stability, age, cycles

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Une connaissance de la réponse dynamique de l'effort de pêche par rapport à l'abondance est essentielle à la compréhension complète des cycles de capture du crabe dormeur dans la Californie septentrionale. Dans cette pêche, il y a décalage entre les variations de l'abondance et le taux de capture, probablement attribuable soit à un décalage entre le temps que les pêcheurs commencent et finissent la pêche après les changements dans l'abondance, ou soit à un décalage dans l'expansion et le resserrement du marché après les changements dans l'abondance, soit à une combinaison des deux facteurs. Le retard de la réaction semble avoir diminué au cours des 30 dernières années. Cette réaction décalée est une cause potentielle de ces cycles. Toutefois, ni l'un ni l'autre des deux processus cycliques potentiels, soit une relation prédateur–proie (où l'homme est le prédateur) et une relation d'écoulement dépendante du prix (où le prix dépend des prises antérieures) n'est la cause de ces cycles. Quoique l'effort variant avec le temps ne cause pas ces cycles, il a une incidence importante sur le total des prises et la dynamique des populations. Si un processus de recrutement dépendant de la densité existe dans cette population, comme il a déjà été suggéré, la réaction décalée ferait que la période des cycles observés serait plus longue que ne le portait à croire

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la seule dynamique de la population. Donc, les évaluations antérieures de la période attendue des cycles d'après les divers processus relatifs aux populations sont faibles. L'élimination de la réaction est un moyen potentiel de stabiliser la pêche.

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THE catch record of the northern California Dungeness crab (*Cancer magister*) fishery is composed of cyclic fluctuations whose cause is not known. Although previous studies have focused on density-dependent (Botsford and Wickham 1978; McKelvey et al. 1980; Botsford 1981; McKelvey and Hankin 1981) and environmental (Peterson 1973; Botsford and Wickham 1975) phenomena as potential causes, little attention has been paid to changes in effort as a possible underlying mechanism. Methot and Botsford (1982) have recently shown that fishing mortality varies in a regular pattern with regard to catch. Fluctuations in effort are of interest not only because they are a potential cause of cyclic fluctuations in catch, but also because knowledge of the factors that determine effort each year (i.e. the dynamic behavior of fishermen, processors, and markets) is required to understand population dynamics adequately and to formulate fishery management policy.

The analysis described here was undertaken to (a) describe the dynamic response of effort to abundance and (b) determine the effect of that response on the fishery. First, the behavior of this fishery and the available data are described. Then possible mechanisms underlying the dynamic response of harvest to abundance are inferred by comparing actual behavior with expected behavior from proposed likely mechanisms. The possible effects of this response on population stability are then evaluated for several different assumed descriptions of population dynamics. In this context, the effect of the harvest response on the previously developed model with density-dependent recruitment is determined.

The Fishery

While the general behavior of the northern California Dungeness crab fishery can be readily described, the mechanisms that actually determine effort in the fishery are poorly known. The fishing season extends from December through June or July and only males larger than 159-mm carapace width can be landed. In most years more than 70% of the legal crabs are landed (Methot and Botsford 1982). Most of the landings are made in the first few months of each season. This is especially true in more recent years. As abundance has fluctuated there have also been fluctuations in price, number of boats, and actual harvest rates. The factors that govern the entry and exit of boats in the fishery during each season govern the fraction of crabs harvested each year.

There are a number of economic factors that could affect the number of crabs landed each year. The price at the beginning of the season is based on negotiations between fishermen and processors, and prices also change during the season. Processors have limited the number of boats and their landings during the recent periods of high abundance and the period of high abundance in the 1960s (D. Gotshall, P.O. Box 98, Avila Beach, CA 93424, personal communication). Average seasonal price generally varies inversely with catch and has increased over the past 30 yr, even when deflated to 1967 dollars by the consumer price index (Fig. 1).

The total number of boats landing crabs each season varies positively with catch with a small lag and has also increased over the past 30 yr (Fig. 2). However, this lag appears to have decreased in recent years. The fluctuation in number of boats in the fishery is related to the high mobility of the fleet; most of these boats also fish salmon and albacore. The number of boats in the fishery unfortunately is not necessarily a direct indication of annual fishing mortality. The actual pattern of harvest rate [based on annual catch and estimates of preseason legal abundance (Methot and Botsford 1982)] is also shown in Fig. 2.

Response of Harvest Rate to Abundance

The way in which harvest rate responds to changes in abundance can have a profound effect on the population. To interpret this response better, we first review the expected effects of the several different bioeconomic mechanisms known to be operating in the fishery, then compare the actual harvest rate record to these theoretical possibilities. From this comparison we can infer the possible mechanisms operating in this fishery.

Behavior of the fishery can be viewed in terms of a static relationship that changes only very slowly (e.g. with long-term changes in price) and a dynamic relationship that reflects the way in which the static "equilibrium" is reached after rapid changes in abundance. If the fishery were given enough time (i.e. a long enough season), the static equilibrium would be approached. At that time, a reasonable model would be that the value of a day's catch would equal the cost of obtaining that catch. Remaining abundance (escapement) would then be inversely proportional to price. From Fig. 1 price varies inversely with abundance. Hence escapement would increase with increasing abundance. The change in harvest rate with abundance would be

$$(1) \quad H = 1 - E(A)/A$$

where H = harvest rate, A = abundance, $E(A)$ = escapement at abundance A. The form of this static, equilibrium relationship between harvest and abundance is determined by the relationship between price, abundance, and escapement. For example, if the inverse relationship between price and abundance caused escapement to increase linearly with abundance, harvest rate would be constant. This relationship will change with long-term changes in price. If real price increases more rapidly than operating costs, escapement levels will decrease; hence harvest rates will increase.

Although this static equilibrium can be at least conceptually defined, it may rarely actually be reached because seasons are

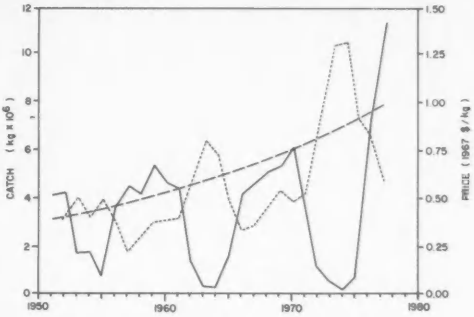

FIG. 1. Annual catch (—) and price (---) scaled for inflation (i.e. 1967 U.S. dollars). The exponential trend that was fit through these data and used to compute adjusted price is also shown (— — —).

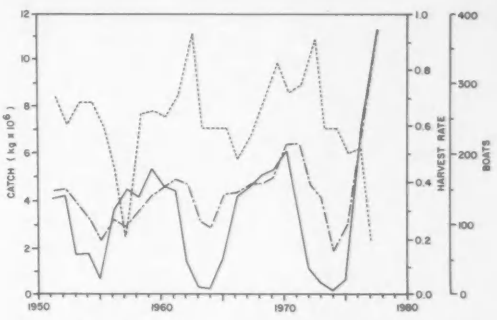

FIG. 2. Annual catch (—), total number of boats making deliveries (— · —), and harvest rate (---) computed from independent estimates of preseason abundance for the northern California crab fishery (Methot and Botsford 1982). (Note: abundance estimates for several years of high abundance (1957, 1966, 1977) were not significant. Hence, although abundance in these years is known to be very high and the values of harvest rate therefore low, the exact values of harvest rate used here are somewhat arbitrary.)

not infinitely long, and fishing capacity and market capacity can limit removal rates. In brief, there may not be enough effort to reach equilibrium before the season closes. If there is not enough fishing capacity (i.e. total boats or total crab pots), a rapid increase in abundance will result in initial low annual harvest rates that increase as more boats enter the fishery. Conversely, a rapid decrease in abundance will produce an initial increase in annual harvest rate followed by a decline. The overall effect would be counterclockwise rotation of the plot of harvest rate and abundance as shown in Fig. 3.

The precise dynamic behavior of this mechanism depends on such factors as price, opportunities in other fisheries, and the capacities of boats in the fleet. If price is high, one would expect that fishermen would maintain the ability to enter the fishery rapidly when abundance increases. Hence a long-term increase in mean price would be expected to result in less dynamic variation about the static equilibrium (i.e. less lag).

In addition to the influence of a lagged response of fishing capacity, a lagged market capacity can affect the harvest rate response in a similar way. As described earlier, processors change prices within seasons and also limit landings directly. During most years there are very few processors buying crab in each port. Few buyers operating under imperfectly competitive conditions characterize an oligopsonistic market. Each is keenly aware of the actions and reaction of the other buyers in the industry. Processing firms can expand and contract their activities in selected fisheries depending on potential profitabilities. Thus, they may respond to available abundance (supplies) in ways to maximize profits, entering a fishery when attracted by high profits, and vice versa. This behavior affects the effort response of the fishery. Suppose that the demand for crab by processing firms in an industry can be represented by the lower-most demand curve (identified as D_{normal}) shown in Fig. 4. If abundance (supply) is relatively low, price will be higher and quantity demanded lower, than under conditions of high abundance. Thus, if abundance has been low and then increases, processors will offer lower prices and purchase larger quantities. Other firms may then be attracted by the profitability of processing crab; their entry essentially shifts the demand curve to the right, increasing price paid to fishermen who respond to the price incentive by harvesting increased quantities. When abundance declines, the supply curves may shift leftward from $S_{\text{high abundance}}$ to $S_{\text{low abundance}}$, along the same demand curve. Prices continue to increase until enhanced profitability is exhausted, the marginal firms or plants exit the industry, and the demand for crab from the fishery shifts back to D_{normal} from D_{expanded}. The market contracts, and both prices paid to fishermen and quantity purchased by processors, fall. The dotted time path within Fig. 4 approximates the locus of prices and quantities over time caused by changes in abundance and the behavior of processors.

The effect of this mechanism on the harvest rate dynamics is a decrease in harvest rate following a rapid increase in abundance. As abundance remains high, catch increases because of market development, and harvest rate increases. When abundance decreases rapidly, catch decreases and harvest rate and price increase. As abundance remains low, price gradually decreases as the initial demand curve is approached, and harvest rate decreases. Thus the effect of this mechanism on the harvest rate versus abundance plot is indistinguishable from the response that resulted from a lagged fishing response. (The effect of a processor-imposed limit on landings is essentially the same as that of limited fishing capacity.) It can be distinguished, however, on the basis of the required increase and decrease in price within the high and low abundance periods, respectively. This pattern appears to be present in the high catch periods in the late fifties and sixties and the low catch periods in the early sixties and seventies (Fig. 1).

A third potential dynamic mechanism is of a completely different nature. It would occur under conditions such that fishing capacity was high enough to fish the legal population down each year to the price-determined level of escapement. However, a lag in the response of price to abundance would prevent the simple, static equilibrium described earlier. If price did not respond immediately to abundance, the response

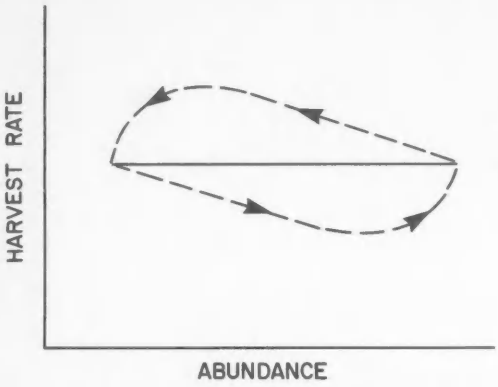

FIG. 3. A typical example of the static, equilibrium relationship between harvest rate and abundance (—) and the path that a fishery with a lagged effort response would follow (---).

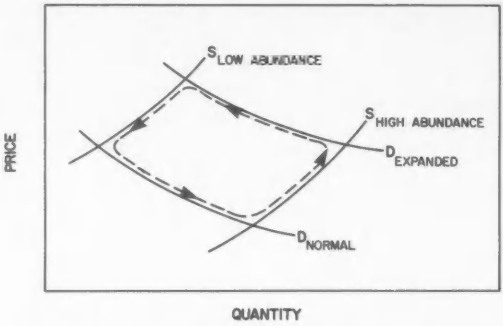

FIG. 4. Proposed changes in supply and demand curves with abundance. When moving between low and high equilibria the system moves initially along the appropriate demand curve (---). This curve shifts as high or low abundance is maintained.

of harvest rate to changes in abundance would be altered in a way that differs from those described previously. The response of price to changes in abundance could be delayed for reasons such as large stocks of frozen crabs held over from previous years.

A rapid increase in abundance with no change (or a slow change) in escapement (because of the slowly changing price) would lead to an initial increase in harvest rate followed by a decline to equilibrium as price decreased. The converse would occur following a rapid decrease in price, resulting in the clockwise rotation of the harvest rate, abundance plot shown in Fig. 5.

MECHANISMS PRESENT IN THE FISHERY

The plot of observed harvest rate and abundance (Fig. 6) does not follow a line of constant harvest rate but rather appears to rotate in a counterclockwise direction. Rapid increases in abundance (e.g. 1957, 1966) lead to low harvest rates, and rapid decreases in abundance lead to high harvest rates (e.g. 1962, 1972). As stated earlier, it is difficult to discern between a lag in fishing capacity and a lag in market capacity as the underlying cause of this behavior. However, the increase in price during periods of high abundance and decrease in price during periods of low abundance is commensurate with a lagged market response. As the observed behavior may be caused by either mechanism, they will be referred to collectively as a lagged effort response in the remainder of this paper.

The higher than usual value of the 1976 harvest rate is commensurate with the increase in real price of crabs. This could have resulted from a more rapid response of effort to increasing abundance because crabs were more valuable.

Any effect of lagged price on escapement is not significant enough to be apparent. The presence of a lagged response of price can be tested for in the price and catch data in Fig. 1. The correlation between adjusted price (1967 dollars with exponential trend removed, Fig. 1) and crab catch in previous years is significant at the 0.05 level at lags of zero and 1 yr but not at 2 yr (-0.739 and -0.453 and 0.063 at lags of zero, 1, and 2 yr, respectively). However, this correlation could stem from a negative correlation coefficient in year zero and highly autocorrelated catch. The partial correlation coefficient implies that the latter is the case. The partial correlation between price at time t and catch at time t given catch at time $t-1$ is significant but the partial correlation between price at time t and catch at time $t-1$ given catch at time t is not significant (-0.590 and -0.085, respectively).

Effect of Harvest Response on Fishery Behavior

The description of the response of harvest rate to changes in abundance can now be combined with descriptions of possible population behavior to determine the effect of harvest response on population level and the fishery as a whole. We will determine whether the harvest response is the cause of the observed cycles through either a predator–prey mechanism or price-dependent escapement with a lagged response of price to abundance, then evaluate the effect of harvest response on a population with density-dependent recruitment.

PREDATOR–PREY CYCLES

Predator–prey cycles with man as the predator involve the following sequence of events: abundance increases, effort increases after a certain lag, abundance then decreases as a result of increased effort, effort decreases in response to decreased abundance after a time lag, and finally, because of decreased effort, abundance increases to begin the next cycle. Both a lagged response of effort to abundance and a lagged response of abundance to effort are required. Mechanisms of this kind have been associated with cyclic behavior in other exploited populations [e.g. Gulland (1974), p. 17; Wilen (1976); Bell et al. (1977)].

Because a lagged response of effort to abundance has been shown to exist, we shall evaluate whether that mechanism can cause the observed cycles in a predator–prey fashion. Abundance each year will be the sum of recruitment and the result of escapement in the previous year. This can be represented by:

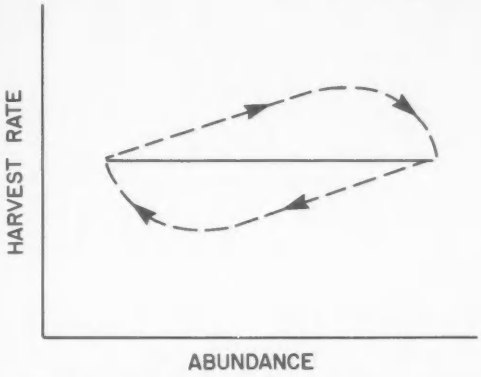

FIG. 5. The static, equilibrium relationship between harvest rate and abundance (—) and the path that a fishery with price-dependent escapement with price dependent on past catch would follow (---).

$$(2) \quad A_t = A_{t-1}(1 - H_{t-1})\,G + R_t$$

where A_t = abundance in year t
H_t = harvest rate in year t
G = total change in biomass during a year (includes natural mortality and growth)
R_t = recruitment to legal size during the year prior to fishing season t.

For this simple representation, age structure is not included. Thus the major simplification of the model is that G is assumed constant when it would in general change with age structure.

This equation can be written in terms of the rate of increase

$$(3) \quad r = A_t/A_{t-1} = (1 - H_{t-1})\,G + R_t/A_{t-1}.$$

In a cyclic population, changes in the values of H_t and R_t must cause the population to shift repeatedly between increasing and decreasing population size ($r > 1$, $r < 1$). Thus, whether this population is cyclic depends on the dependence of harvest rate on past abundance (described earlier) and the dependence of recruitment on abundance. We now evaluate the combination of harvest rate behavior described earlier with two different assumptions regarding recruitment: constant recruitment rate and recruitment rate proportional to abundance. (Density-dependent recruitment is evaluated in the next section.)

If recruitment rate is proportional to population size, in predator–prey cycles the population will increase from low levels because decreasing harvest rate is allowing a larger population to build up. If this were happening, there would be greater escapement at lower abundance. From Fig. 7 this is not the case. Higher escapement occurs at higher abundance.

If recruitment rate is constant in predator–prey cycles, the change in harvest rate itself must cause the shift between an increasing and a decreasing population. This does not appear to be the case because of the way that abundance changes. At low levels harvest rate drops from near 0.9 to near 0.5 with no change in abundance, then abundance suddenly increases.

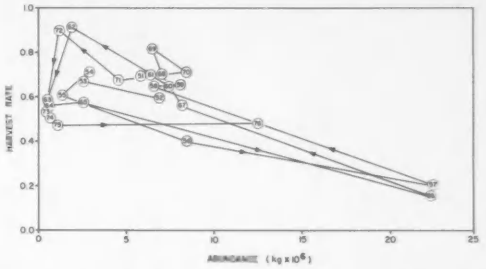

FIG. 6. Actual annual harvest rates plotted versus actual abundance for the northern California Dungeness crab fishery. (Because abundance estimates for 1957 and 1966 were not significant, the exact position of these points is somewhat arbitrary. However, abundance was unusually high and harvest rate was unusually low.)

There is again no gradual increase in abundance evident in the escapement at low levels.

The only remaining alternative is that recruitment is higher at low population levels and vice versa (i.e. density-dependent). Again the lack of gradual increase in population level (escapement) at low levels implies that for this mechanism to be significant a lagged response of recruitment to abundance is required. However, even if that were the case, it does not seem likely that the slight changes in harvest rate seen here are enough to be controlling abundance. The changes in harvest rate at high abundance levels are not large enough to cause the observed declines in abundance. Thus, even though a lagged recruitment response may be present, it does not appear to interact with harvest rate to cause predator–prey cycles.

From these considerations we can conclude that changes in harvest rate in response to abundance are not the primary cause of fluctuations in abundance in a predator–prey fashion. However, we have not discounted the possibility that they may influence population behavior significantly by exacerbating instability caused by other mechanisms.

PRICE-DEPENDENT ESCAPEMENT WITH LAGGED PRICE RESPONSE

Though there was little evidence for a lagged response of price to past catch or abundance and the behavior of price-dependent escapement with a lagged price response did not appear to be dominant in Fig. 6, analysis of stability of this mechanism is presented briefly because it may apply to this fishery in the future or to others. If escapement depended inversely on price, as described earlier, and price was influenced by previous catch (e.g. due to storage of past catch by processors and marketers), then catch could be cyclic. As abundance increased, high catch would lead to low prices which would result in high escapement and low catch. When abundance decreased, low catch would eventually lead to high prices which would result in low escapement and high catch, and the cycle would then repeat.

To analyze stability of this mechanism, we assume that escapement each year depends (possibly in a nonlinear fashion) on a weighted sum of total catch in previous years.

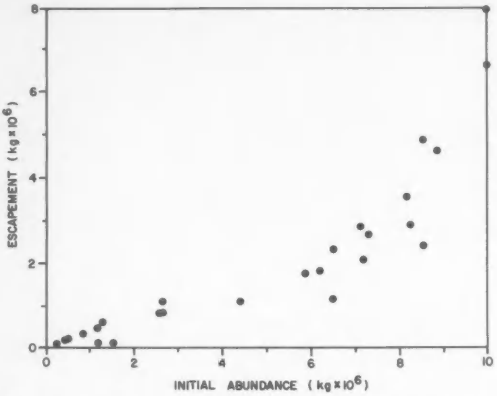

FIG. 7. Annual escapement and initial abundance estimates for the years 1955 through 1976 in the northern California Dungeness crab fishery.

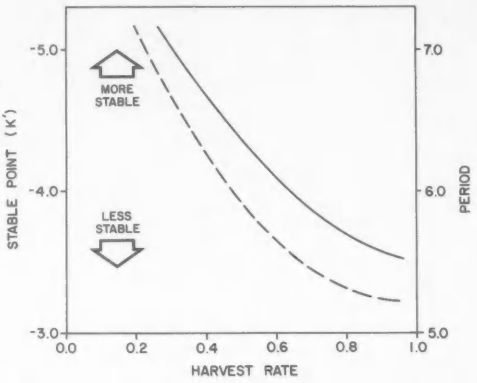

FIG. 8. The stable point K' (---) and the period of cycles produced (—) for a discrete time model with density-dependent recruitment as the (constant) annual harvest rate is varied.

$$(4) \quad (1 - H_t)\, A_t = g\left[\sum_{s=1}^{T} k_s\, H_{t-s}\, A_{t-s}\right]$$

where k_s = a constant specifying the relative effect of catch in the sth previous year on escapement in the current year ($s = 1, 2, \ldots T$). In the crab fishery, for example, g would be an increasing function of its argument (i.e. as catch in previous years increases, market price is depressed and escapement increases).

By defining catch to be

$$(5) \quad C_t = A_t\, H_t,$$

we can express the equations (2) and (4) as

$$(6) \quad C_t = Gg\left[\sum_{s=1}^{T} k_s C_{t-1-s}\right] - g\left[\sum_{s=1}^{T} k_s C_{t-s}\right] + R_t.$$

This expression has the intuitively satisfying interpretation that catch is growth per unit biomass (G) times last year's escapement minus this year's escapement plus this year's recruitment (R_t). The fact that catch is the weighted difference between two lagged escapements critically affects dynamic behavior of this system.

The derivation of the conditions under which this model would be unstable and the catch record that would result are in the Appendix. The relevant result here is that for a wide range of reasonable forms of the dependence of price on past catch, any unstable cycles produced will be of period two. Intuitive support for this result can be gained from equation (6). Catch depends on the difference between a function (g) of past catches at different time lags (time lags in the first term are shifted backward in time by 1 yr with respect to time lags in the second term). Because of this, in the dynamic behavior of this system each lagged catch is approximately cancelled by its corresponding component in the other term. There is only one term left uncancelled, the term involving catch at a lag of 1 yr. Only cycles of period two can result from a lagged response at 1-yr lag.

A second result of this analysis is that if price depends significantly on the present value of catch in addition to past values of catch, the system becomes much more stable. Because of these two results, it is not likely that this mechanism is causing the observed periodic fluctuations in catch.

Density-Dependent Recruitment

Density-dependent recruitment is one of the possible causes of the observed cycles in the northern California crab population. The stability and behavior of an age-specific model with density-dependent recruitment and constant effort were analyzed by Botsford and Wickham (1978) in relation to this population. However, the results obtained by them assumed constant effort, hence, do not hold for the time-varying effort identified here. To determine whether the density-dependent recruitment mechanism is present in this population, the behavior of a model that includes the dynamic response of effort to abundance must be known.

The results obtained by Botsford and Wickham (1978) were in terms of (a) the stability inherent in the age structure of the population and (b) the period of cycles produced. In their model recruitment was the product of total reproduction and a recruitment survival function that depended on effective population size. Stability depended on the relative values of the normalized slope of the density-dependent recruitment function (i.e. the amount that the recruitment survival function changed with a change in population size) and the inherent stability of the population age structure. The general result was that a population with a greater number of age-classes was usually more stable (i.e. could tolerate a steeper slope of the recruitment survival function) than a population with fewer age-classes. The period of the cycles was shown to be roughly twice the mean lag between the age at which the inter-age, density-dependent effect acts on younger animals and the age at which older animals cause this effect (i.e. approximately the mean age of those individuals causing

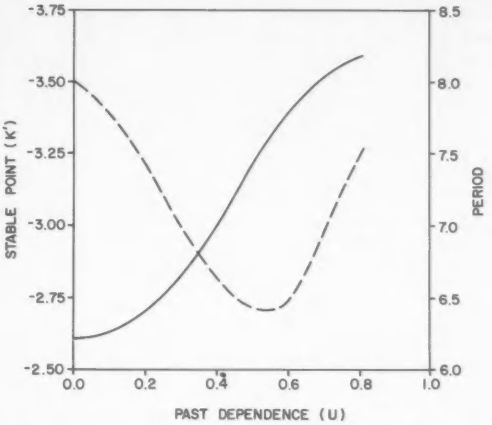

FIG. 9. The behavior of the stable point K' (---) and the period of cycles produced (—) by the discrete time model with density-dependent recruitment with constant effort replaced by a lagged response of harvest to abundance as the degree of lagged response is varied from $U = 0$ (constant effort) to higher values.

density-dependent recruitment).

These characteristics are reflected in the values of period and stable point obtained through simulation of a discrete-age version of the baseline model (with reproduction) presented in Botsford and Wickham (1978) (Fig. 8). The stable point K' is the minimum value of slope of the density-dependent recruitment function that can be tolerated before the population becomes unstable. Hence, a more negative value of K' corresponds to an inherently more stable population. As the level of constant effort increases, the relative number of age-classes decreases (i.e. older age-classes are depleted), and the population becomes less stable. Also, because the mean age of the population decreases with increased effort, the period of the cycles decreases.

Though we don't know the specific mechanism causing the response of harvest rate to abundance, we can evaluate the effect of this response on population stability through a simple model that mimics harvest rate dynamics. Define

$$(7a)\quad C'_t \equiv H_{\text{norm}} A_t (1 - U) + C_{t-1} U,$$

$$(7b)\quad \text{then let } C_t = C'_t \qquad C'_t < H_{\max} \times A_t$$

$$(7c)\quad C_t = H_{\max} A_t \qquad C'_t \geq H_{\max} \times A_t$$

where U = a constant $(0 \leq U \leq 1.0)$
C_t = catch in year t
A_t = abundance in year t
H_{norm} = equilibrium harvest rate
$H_{\max}$ = maximum harvest rate.

In this model, catch is a weighted sum of abundance harvested at a rate of H_{norm} and last year's catch (7a), except that harvest rate is constrained to be less than $H_{\max}$ (7b and 7c). The constant U reflects the relative dependence of harvest rate, and therefore catch, each year on the previous year's catch (i.e. the relative inertia or lag in the response).

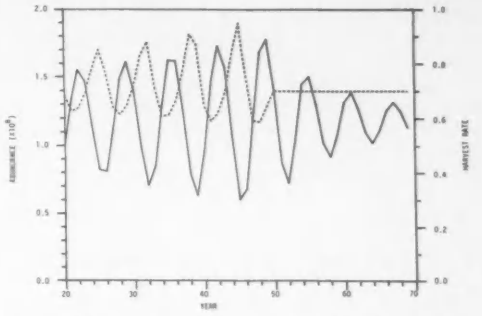

FIG. 10. An example of increased stability through removal of a lagged effort response. Catch (—) and harvest rate (---) are initially fluctuating in an unstable fashion. When harvest rate is set to a constant value for $t > 60$ yr, the population becomes stable.

For values of H_{norm} and $H_{\max}$ that produce a typical pattern of harvest rates, as the value of U is varied from 0.0 (a constant harvest rate) to higher values (greater past-dependence), the period of the cycles produced increases (Fig. 9). The inherent stability of the model also decreases up to $U = 0.8$ at which it increases. Because it is not likely that current catch depends to such a large degree on past catch, this value is probably beyond the values that produce a reasonable model of the actual response. Thus, over the reasonable range of values, stability decreases with increased dependence of the effort response on previous catch.

Discussion

The dominant response of effort in this fishery over the past 30 yr is one of considerable inertia or resistance to rapid change. The dramatic increases and decreases in abundance are not perfectly "tracked" by the catch record. This effect is caused by two limitations on the rate of "outflow" from the population to the consumer. The first is the limited number of boats or crab pots. Because of the limited capacity of each boat, catch cannot change dramatically until the number of boats or pots changes. The second limitation is the rate at which processors will accept crabs. This rate is prevented from changing rapidly by economic factors. The relatively small number of firms in the industry can engage in collusion to protect or increase profits by limiting quantities. As these two limiting mechanisms, fishing capacity and market capacity, operate in series, either one of them can be the "limiting factor" at different times.

The lack of significance of a price-dependent escapement mechanism with past-dependent price is somewhat unexpected. Escapement does appear to increase with the inverse of adjusted price as would be expected if the population were reduced to the zero-profit level each year. That the plot of harvest rate versus abundance (Fig. 6) does not reflect this type of fishery is primarily because of the years following a rapid increase or a rapid decline in abundance (i.e. 1956, 1966 and 1962, 1972). The dependence of price on past catch is expected because of the stores of frozen crab that are left from

year to year in processors' lockers. A possible explanation for the absence of this relationship is that a prediction of abundance (based on a preseason cruise) was available before the price negotiations that preceded each season. This could have shifted dependence on past catch to dependence on the (expected) present catch. A second possibility is the adjustments in price that are made during most seasons. They would also shift price-dependence toward the present.

The lagged effort response in this fishery appears to be less prevalent in recent years. This would be expected on the basis of the increase in real price. (The general increase in real price is not confined to this fishery but has also occurred in others in recent years.) As price increases, the lag in response of fishing capacity will decrease because of the increasing advantage of maintaining the ability to enter the fishery rapidly. The increasing value of crabs will also induce other processors to enter the fishery, thus decreasing the lag associated with market response.

The trend in the influence of effort response on this fishery appears to be generally toward increasing stability. Decreased lag increases stability of predator–prey mechanisms and the density-dependent recruitment mechanism. The fact that instability can arise with no lag in effort, because of the price-dependent escapement mechanism with past-dependent price, does not contradict this general trend. Instability from this mechanism is of a special kind. It occurs in what would be a stable region in continuous time and is possible only because this system is defined in terms of discrete time. This is reflected in the fact that cycles arising from this mechanism would be of period two. Thus, the overall trend is toward greater stability.

Other mechanisms may influence effort in this fishery. Botsford et al. (1982) analyze a cyclic covariation of California salmon catch with crab catch. Salmon catch peaks when crab catch is increasing. Because crab and salmon seasons do overlap, high salmon catch could contribute to low harvest rate during years of increasing crab abundance. Also, in recent years, limitations on entry into other fisheries have induced fishermen to make a couple of landings in fisheries that are not yet limited (such as the crab fishery), merely so that they can maintain the option of later participating in that fishery on a larger scale even if entry is eventually closed.

The impact of the lagged response on stability of a population with density-dependent recruitment is relevant both to the issue of the cause of the cycles and future management of the fishery. The stability results obtained seem intuitively reasonable. Earlier work using constant effort showed that stability increased as effort decreased causing the relative numbers in older age-classes to increase. The period also increased as the numbers in older age-classes increased. As one replaces constant effort with a lagged response of effort to catch, one would expect a decrease in stability because a lagged feedback system is being allowed to overshoot the equilibrium by a greater amount. Conversely, a decrease in the lagged effort response allows less overshoot, hence would be expected to stabilize the system. This reasoning holds until the lag becomes so great ($U = 0.8$) that the increased overshoot allows a substantial increase in the number of older individuals in the population. From the constant effort results, we know that this acts to stabilize the population.

The results in Fig. 9 appear to be robust to variations in H_{max} and H_{norm} over ranges of values that match observed harvest rates. Slight variations in H_{max} do not substantially change results. Varying H_{norm} to 0.5 or 0.7 produces a less stable population at 0.7 and a more stable population at 0.5, as would be expected on the basis of constant effort results (Fig. 8). The pattern of changes in stability as U is varied is preserved.

The new result, that the period of cycles produced by density-dependent recruitment increases with a lagged effort response, has important implications for the determination of the cause of the cycles. Botsford and Wickham (1978) noted that the period of observed cycles was greater than the period of cycles produced by a model with constant effort, current estimates of life-history parameters, and the density-dependent recruitment effect occurring near the time of post-larval settlement. The last characteristic would be the case if cannibalism were the density-dependent mechanism. McKelvey et al. (1980) pointed out the same disparity between model periods and observed periods, using a different model with discrete time and age. They chose, however, to reject cannibalism as a potential cause of the cycles on that basis. [See Botsford (1981) and McKelvey and Hankin (1981) for further discussion.]

The fact that the observed lagged effort response can cause an increase in period of 25% (Fig. 9, constant effort versus $U = 0.6$) is an example of a previously unknown mechanism that can have a significant effect on the period of observed cycles. As such, it underscores the potential hazards of rejecting mechanisms because they do not satisfy a certain model when it is not known whether the other parameters and structure of the model accurately mimic the real population (Botsford 1981). Thus, this result casts doubt on both the specific rejection of cannibalism as a cause of the cycles by McKelvey et al. (1980) and the general form of argument used in doing so.

A second feature of the stability results is their potential use in management. The fact that removal of a lagged response can make the population more stable leads directly to consideration of employment of this fact in management. If the amount of effort (or catch) could be increased over its present value during high years and possibly lowered during low years, the population could stabilize at a constant value. The increase in effort following an increase in abundance could possibly be brought about by better prediction of good years and early market development or reduction of the oligopsonistic nature of the fishery. (The latter would probably increase overall value of the fishery even if stability were not affected.)

The potential effect of this behavior can be demonstrated by simulating the fishery using a lagged effort response [equation (7)] then switching to constant effort (Fig. 10). In this example, removal of the lagged effort response caused the population to become stable. The actual change in harvest policy required to stabilize the crab fishery (if it is possible) requires further definition of the population and the fishery. The possible policies examined should not be confined to those that would return the system to constant harvest rate but rather should include schemes which go beyond that to policies that include higher harvest at high abundance and lower

harvest at low abundance. Other simulations have shown that these policies can have an even stronger stabilizing effect than just removing the lag.

This scheme would be beneficial in spite of the fact that the actual cause of the cycles is unknown. If the cycles were caused by environmental factors rather than density-dependent recruitment, long-term landings from the fishery would probably be increased even though the population would not stabilize at a constant value. A policy such as this could also serve as a test of several potential causes of the cycles. If the population were stabilized by such a policy, then density-dependent mechanisms that involve only the unfished females and mechanisms involving the environment could be rejected. A gratuitous observation on the stabilizing effects of diminished lag is that the decrease in lag that has accompanied the long-term increase in market price could possibly stabilize the fishery without actual policy changes.

The influence of a lagged fishery response on stability of models with density-dependent recruitment has shed some light on mechanisms underlying cycles and provided a potential management approach. However, both the identification of the cyclic mechanism and the eventual advisability of such a management scheme depend critically on further definition of the life history parameters of the crab and the influence of environmental variables on this population.

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Appendix

The approach to stability analysis is to determine conditions for local stability of a linearized version of the model in terms of small variations about an equilibrium point. If the linearized model is stable, the model is locally stable. If the linearized model is unstable, the model is locally unstable. The condition of equilibrium, assuming recruitment, is

$$\text{(A-1)} \quad C_e = g\left[C_e \sum_{s=1}^{T} k_s\right](G-1) + R_t.$$

From the definition of a small variation in catch about equilibrium,

$$\text{(A-2)} \quad \Delta C_t = C_t - C_e$$

and from equations (6) and (A-1) the linearized model can be expressed as

$$\text{(A-3)} \quad \Delta C_t = g'\left[C_e \sum_{s=1}^{T} k_s\right] \sum_{s=1}^{T+1} h_s \Delta C_{t-s}$$

where $g'(x) = dg(x)/dx$

$$h_s = -k_1 \qquad s = 1$$
$$h_s = -k_s + Gk_{s-1} \qquad 1 < s < T$$
and $$h_s = Gk_T \qquad s = T.$$

The coefficients (h_s) of lagged values of the variation in catch are the difference between the coefficients (k_s) describing the influence of past values of catch on escapement and G times these same coefficients lagged by one time interval. This implies that if the values of k_ss decrease by a certain fraction for each interval (i.e. $k_{s+1} = pk_s$, $0 \le p \le 1$), for values of p near the value of G, h_s is very small for all $s > 1$. Stability will than be determined by k, and the system will behave as one that depends only on the past year's catch. Stability conditions for this simple case are similar to other familiar models (e.g. the single age-class stock–recruitment model). The system will be stable if $g'k < 1$, unstable if $g'k > 1$, and the response will be cyclic with period 2 yr.

Determination of stability for cases other than this simple case is more difficult. If escapement depends on catch up to n yr in the past, analysis of an nth order system is required. However, by assuming that the dependence of escapement on past catch decreases by a fixed proportion each year, we can simplify the analysis considerably.

We define a new variable S_i that could physically be the biomass of crabs in storage for i yr. We then assume that the amount in storage decreases by a fixed proportion each year

(A-4) $S_i = p^i C_{t-i}$.

This enables us to express the system in terms of only two variables S_1 and

(A-5) $$S = \sum_{i=1}^{t-1} p^i S_i.$$

The equations describing the system are

(A-6) $S_1' = g[S]G - g[pS_1 + pS]$

(A-7) $S' = p(S_1 + S)$

where the primes denote values in the current year and unprimed variables refer to the values in the previous year.

From the modified Schuur–Cohn criterion (Freeman 1965), also called the Jury test (Lewis 1977), we obtain the necessary and sufficient conditions for stability.

(A-8) $$g' < \frac{1 - p}{-p\,(2p - 1 - G)}$$

and

(A-9) $$g' < \frac{1 - p}{p|2p - G|}.$$

The system will be unstable if either of these is violated. Note that for $p = G$, the first condition reduces to $pg' < 1$, the same condition as arrived at above from the observation that the system would behave as if there were only a single lagged response after 1 yr. From equations (A-8) and (A-9), stability of this model depends on the relative values of G, g', and p. As stated earlier, p, the fraction of stored stock not sold each year, varies between 0.0 and 1.0. The value of g', the change in escapement with a change in past catch, is positive for a compensatory relationship between escapement and past catch. The value of G, the relative growth rate of biomass from 1 yr to the next, depends on growth and survival of the species as well as fishing effort.

Stability conditions [equations (A-8) and (A-9)] were verified by simulation for a range of values of p. Values of G were computed from estimates of growth and survival rate of the crab population (Botsford and Wickham 1978). Unstable behavior was always cycles of period two. Addition of the dependence of price on current catch increased stability by a factor of two if the weighting of present dependence was equal to the weighting of catch 1 yr in the past, and by a factor of 10 when the weighting of present catch was doubled. Thus the system is much more stable when price depends on present catch.

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Reliability in Measuring Diet Overlap

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WALLACE, R. K., AND J. S. RAMSEY. 1983. Reliability in measuring diet overlap. Can. J. Fish. Aquat. Sci. 40: 347–351.

Intraspecific diet overlaps were calculated for young-of-the-year largemouth bass (*Micropterus salmoides*), juvenile bluegills (*Lepomis macrochirus*), and inland silversides (*Menidia beryllina*) by randomly dividing collections of each species into two sets, measuring the diet (average of the volume percentage) and calculating the diet overlap by Schoener's method. The randomization process and overlap calculation were repeated 30 times and an upper confidence limit (95%) for intraspecific overlap was determined. Upper confidence limits of intraspecific overlap were generally below the 100% overlap expected if diets were adequately characterized. Intraspecific overlap varied with collection date, fish species, and size of sample. Increasing sample size did not increase intraspecific overlap when the larger sample included a wider size range of fish. The upper confidence limit of intraspecific overlap can be used as a measure of reliability for interspecific diet overlap calculations. We suggest that intraspecific overlaps approaching 100% indicate high reliability for the corresponding interspecific overlap value. The intraspecific overlap is most useful in judging the reliability of interspecific overlap when sample size is limited.

Key words: diet overlap, intraspecific overlap, interspecific overlap

WALLACE, R. K., AND J. S. RAMSEY. 1983. Reliability in measuring diet overlap. Can. J. Fish. Aquat. Sci. 40: 347–351.

Nous avons mesuré le degré de superposition intraspécifique du régime alimentaire d'achigans à grande bouche (*Micropterus salmoides*) de l'année, de jeunes crapets arlequins (*Lepomis macrochirus*) et de capucettes d'eau douce (*Menidia beryllina*). À cette fin, nous avons séparé en deux séries au hasard les échantillons de chaque espèce, mesuré le régime (moyenne du pourcentage en volume) et calculé la superposition des aliments selon la méthode de Schoener. Le processus de séparation au hasard et le calcul de la superposition ont été répétés 30 fois, et une limite de confiance supérieure (95 %) déterminée pour la superposition intraspécifique. Ces limites de confiance sont généralement inférieures à la superposition de 100 % anticipée si les régimes sont adéquatement caractérisés. La superposition intraspécifique varie en fonction de la date de collection, de l'espèce de poisson et de l'importance de l'échantillon. Une augmentation de cette dernière n'entraîne pas une superposition intraspécifique plus grande si l'échantillon plus considérable inclut un plus grand éventail de tailles des poissons. On peut utiliser la limite de confiance supérieure de la superposition intraspécifique comme mesure de la fiabilité des calculs de superposition interspécifique de régime. Nous suggérons que les superpositions intraspécifiques se rapprochant de 100 % indiquent une bonne fiabilité des valeurs de superposition interspécifique correspondante. La superposition intraspécifique est surtout utile pour juger de la fiabilité de la superposition interspécifique avec échantillons limités.

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A number of niche overlap measures (indexes) have been used to quantify diet overlap in fish (Cailliet and Barry 1979; Wallace 1981). Horn (1966) cautioned that such measures are appropriate only in situations where there is confidence that the proportion of items in each food category of the diet is adequately characterized. Little attention has been paid to this warning in measuring diet overlap among fish. This apparent oversight is important because failure to characterize the diet adequately of the fish species in question can result in overlap values which have little or no value.

Overlap indexes generally take values between 0% (no overlap) and 100% (complete overlap). An underlying assumption is that the intraspecific overlap is equal to 100% when the diet is adequately characterized. If intraspecific overlap deviates from 100% then it is less likely that

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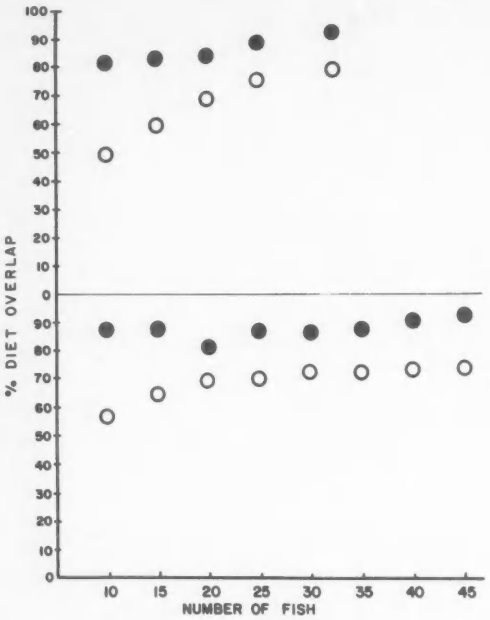

FIG. 1. Upper 95% confidence limit (●) and mean (○) for intraspecific diet overlaps of large bluegills (31–54 mm) (*upper*) and for large largemouth bass (12–16 mm) (*lower*) with increasing sample size.

interspecific values of overlap will be meaningful estimates of true overlap.

The purposes of this paper are to demonstrate that the intraspecific overlap of small samples often deviates from the expected 100% and to suggest a measure of diet reliability which can be used to better understand interspecific diet overlap values.

Materials and Methods

Young-of-the-year largemouth bass (*Micropterus salmoides*), juvenile bluegills (*Lepomis macrochirus*), and inland silversides (*Menidia beryllina*) were obtained from four experimental ponds (0.4–0.8 ha) at the Auburn University Fisheries Research Unit, from April to October 1980, and from False River, Louisiana, in May of 1979 and 1980. Fish were also collected every 4 h for 24 h from three of the ponds on June 1 and 2. Seine hauls were made parallel to and close to shore. Sampling continued until an adequate number of fish were collected, but sampling time did not exceed 1 h per pond. All fish were immediately preserved in 10% formalin and later transferred to 40% isopropyl alcohol. Observations of fish in formalin and subsequent examination of the stomach contents indicated that regurgitation was not a significant problem. Largemouth bass and bluegills, when processed for stomach analysis, were divided into two size groups referred to as large largemouth bass, small largemouth bass, large bluegills, and small bluegills. The 25 smallest and the 25 largest fish of each species were selected for this grouping from each collection. The distribution of sizes in the two size groups was dictated by the fishes present in each collection and no effort was made to standardize the groups from collection to collection as the fish were growing throughout the study. All fish selected for stomach analysis were measured (standard length, SL), blotted dry, and weighed. The stomachs of 20 fish from each of these two size groups and 20 inland silversides were opened and the contents identified (Pennak 1978). The length, width, and depth of each food item was measured to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope, for an estimate of volume.

TABLE 1. Analysis of variance for the 95% upper confidence limit of intraspecific overlap.

Source of variation	Sum of squares	df	*F* statistic	Probability of a greater *F*
Collection date	3843.7	20	2.84	0.0003
Collection site	512.6	3	2.52	0.0608
Species	588.2	4	2.17	0.0774
Site × Species	644.9	7	1.36	0.2295
Number of fish	387.6	1	5.72	0.0186
Error	7045.8	104	—	—

When single food categories were extremely abundant (>50 to 100 or more items in one stomach), they were subsampled and the volumes extrapolated from a count of all the items. Additional fish were examined when empty stomachs were encountered until all 25 fish were sampled. Empty stomachs and some smaller collections prevented uniform samples of 20 fish stomachs but the overall average was 18.7 stomachs per sample (n = 6–20). More than 20 stomachs were analyzed in a few collections to check the effect of increased sample size.

The resulting data from 2658 stomachs (140 samples) were entered into a computer program (SAS, Hewlig and Council 1979) which randomly divided each sample (large largemouth bass, small largemouth bass, etc.) into two sets. Each set was then treated separately so that the intraspecific diet overlap could be calculated. For example, large largemouth bass from a particular pond on a particular collection date constituted a sample. The large largemouth bass were then randomly divided into two equal sets and the diet overlap calculated between the two sets.

Diet overlap was calculated using an index of overlap from Schoener (1970):

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n}\left|P_{xi} - P_{yi}\right|\right)$$

where α is the overlap index, P_{xi} is the proportion of food category i in the diet of species x, P_{yi} is the proportion of food category i in the diet of species y, and n is the number of food categories. The average of the volume percentages (Larimore 1957; Wallace 1981) was the diet measure used in the overlap index.

The randomization and overlap index calculation was re-

TABLE 2. Summary of analysis of variance for the effect of number of fish examined on the 95% upper confidence limit of intraspecific diet overlap.

Collection site	Species and size category	No. of collections	No. of fish (range)	Probability of a greater F
False River	Large bluegills	6	6–18	0.0675
	Large largemouth bass	6	13–20	0.1732
	Inland silverside	6	10–20	0.1129
Pond S-22	Large bluegills	14	10–20	0.0035
	Small bluegills	14	12–20	0.5621
	Large largemouth bass	10	7–20	0.8739
	Small largemouth bass	11	14–20	0.3924
	Large inland silversides	14	16–20	0.0700
Pond S-24	Small bluegills	4	17–20	0.3444
	Small largemouth bass	4	19–20	0.1729
	Large inland silversides	4	10–20	0.4479
Pond S-25	Large bluegills	12	15–20	0.2839
	Small bluegills	10	12–20	0.5990
Pond S-26	Large largemouth bass[a]	11	13–20	0.5957
	Small largemouth bass	11	14–20	0.4676

[a]See Fig. 2.

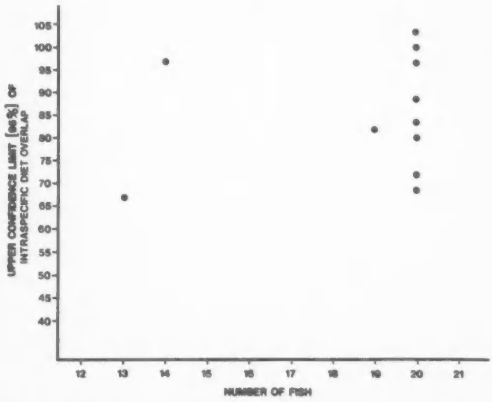

FIG. 2. Relationship between the upper 95% confidence limit of intraspecific overlap for large largemouth bass and number of fish at different collection dates.

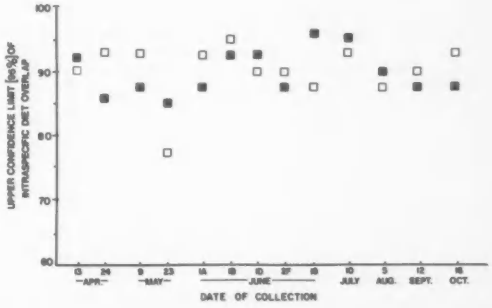

FIG. 3. Upper 95% confidence limits of the intraspecific overlaps of large bluegills (■) (25–56 mm, n = 16–20) and large bluegills plus small bluegills (□) (20–56 mm, n = 35–40) combined, by collection date.

peated 30 times for each sample. The means, standard deviations, and upper confidence limits (95%) of the intraspecific diet overlaps were calculated for the 140 fish samples. The 95% upper confidence limit was then examined by analysis of variance methods (Hewlig and Council 1979) to determine the effect of factors such as collection date, collection site (ponds and False River), species, and number of fish. The 95% upper confidence limit was used because of the widespread use of this probability level and to standardize the maximum intraspecific overlap that might be expected from a sample.

Results

The selection of 30 as the number of replicate randomizations was somewhat arbitrary although the cost of computer time was a consideration. However, a check of the effect of the number of replicates up to 30 for a representative sample revealed that the mean and upper confidence limit varied with increased randomization but appeared to stabilize at 25 trials. When overlap was plotted by number of fish for two samples in which more than 20 fish were available (Fig. 1), the mean intraspecific diet overlap increased with sample size but the 95% upper confidence limits were relatively stable. Straight line projections revealed that larger samples (15–25 additional fish) would be needed for an upper confidence limit of 100% to be reached.

The 140 calculated upper confidence limits of intraspecific overlap ranged from 44 to 108% ($\bar{x}$ = 88.4%). Analysis of variance revealed that collection date, collection site, species, and number of fish contributed significantly ($P < 0.10$) to variation in the upper confidence limit (Table 1). Examination of the effect of number of fish for each combination of species and collection site with more than three collections showed

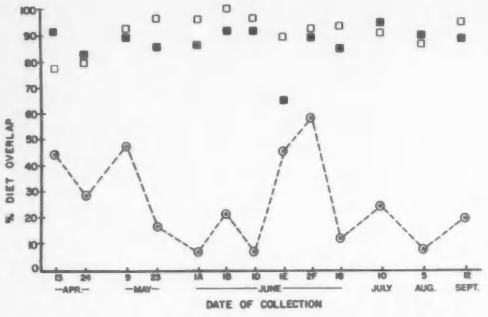

FIG. 4. Diet overlaps (⊙) between large bluegills (28–78 mm) and inland silversides (31–77 mm) and upper 95% confidence limits of the intraspecific overlaps for large bluegills (■) and inland silversides (□) by collection date. 1A...2F are 6-h intervals on June 1 and 2.

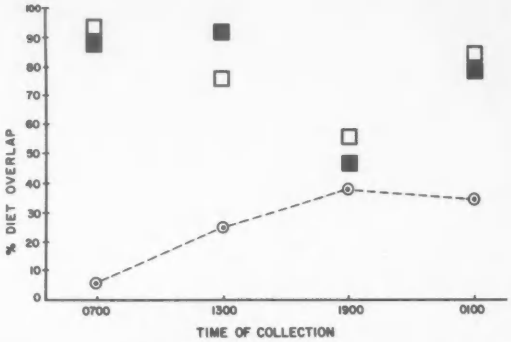

FIG. 5. Diet overlaps (⊙) between large bluegills (25–56 mm) and inland silversides (42–90 mm) and upper 95% confidence limits of the intraspecific overlaps for large bluegills (■) and inland silversides (□) by collection time.

that in 13 of 15 cases, fish number was a poor predictor of the upper confidence limit when number of fish varied from 6 to 20 (Table 2). This is further illustrated by a typical example (Fig. 2).

Because the species were divided into groups of large and small fish, it was possible to assess the effect of this division by recombining the large and small groups, calculating an intraspecific overlap, and comparing this to the overlap of the original groups. Thus the intraspecific overlap of ~40 fish with a wide size range was compared to the intraspecific overlap of ~20 fish with a narrow size range from the collection site with the most samples. Increasing the number of specimens (bluegills) in this manner did little to improve intraspecific overlap (Fig. 3). Seven upper confidence limits were increased in the larger, more heterogeneous sample, whereas six were decreased. Similarly, three upper confidence limits were increased, whereas five were lowered, and one stayed the same when size-classes of largemouth bass were combined.

Discussion

The requirement that the diet of each species be adequately characterized is not easily met, assuming that the intraspecific overlap should be 100%. Diets could be more accurately described by increasing sample size. A method for determining sample size is presented by Hoffman (1979) in which the cumulative diversity of stomach contents is plotted against the number of stomachs examined. When the cumulative diversity appears to have leveled off, the minimum number of stomachs has been examined to characterize the diet. One problem with this method is that many more fish than the minimum sample size eventually determined are needed to calculate the minimum sample size. As shown above, the intraspecific overlap varies with collection date, site, and species. Thus, the minimum sample size determined by the cumulative diversity method for a species at one collection date or site may not be the same for another species, collection date, or site. Strict application of the cumulative diversity index would require that more stomachs be examined for each sample than is necessary. The number of stomachs that can be examined in many studies is often limited by fish availability or by a lack of manpower necessary for analyzing thousands of stomach contents.

Even when sample size is easily increased there still remains the potential problem of increasing the heterogeneity of the sample. This was demonstrated in Fig. 3 where doubling the sample size of bluegills by including a greater size range of fish did little to increase intraspecific overlap over that of smaller samples with a narrow size range of fish.

The intraspecific overlap does not answer the question of how many stomachs need to be examined to characterize the diet adequately. It does, however, give an indication of how well the diet of a species was measured at each collection site and period. Intraspecific diet overlaps that are less than 100% indicate less than adequate diet measurement.

We suggest that, in the absence of a test of sample size, the upper confidence limit of the intraspecific overlap from a randomization process be used to give an indication of the reliability of interspecific overlap calculations. One method of presenting these data is shown in Fig. 4 and 5 where the intraspecific overlaps are presented for each interspecific overlap. When diet overlaps are summarized in tables, the mean and range of the intraspecific overlap might be appropriate.

There are no criteria for judging the reliability of the interspecific overlap even when the intraspecific overlap is known. Some authors (Zaret and Rand 1971; Mathur 1977) have used 60% interspecific overlap as being biologically significant. This intuitive approach might be applied to the intraspecific overlap. If the 95% upper confidence limit of intraspecific overlap is less than 60%, then the diet is poorly characterized and the corresponding interspecific overlap is probably unreliable. When intraspecific overlap is greater than 60%, then increasing reliability may be attributed to the between-species overlap. Figure 3 shows intraspecific overlaps that are generally above 80%, and it is reasonable to assume that the corresponding interspecific overlaps are fairly reliable. However, intraspecific overlap observed in sample 1E (Fig. 4) for bluegills is 63%. This meets the suggested 60% criterion but it would be unwise to attach great importance to the corre-

sponding interspecific overlap. Figure 5 shows an intraspecific overlap of less than 60% for both species at the 1900 hour collection. Certainly no importance should be attached to this particular interspecific overlap as the diets of each species are so poorly characterized.

Good technique dictates that samples of sufficient size be collected in the first place as determined by a method such as that suggested by Hoffman (1979). The realities of sampling fish for stomach analysis warrant an ex post facto test of the adequacy of a sample. Diet overlap values from small samples may have little meaning without a measure of reliability. This is especially evident in view of the high variability of the upper confidence limit when compared to the number of fish in small samples (Fig. 2). The intraspecific overlap based on an upper confidence limit for each sample gives an indication of how well the diet is characterized and a measure of the reliability of the interspecific overlap.

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A New Method for Allotting Effort to Individual Species in a Mixed-Species Trawl Fishery

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WESTRHEIM, S. J. 1983. A new method for allotting effort to individual species in a mixed-species trawl fishery. Can. J. Fish. Aquat. Sci. 40: 352 – 360.

A new method is described which allots fishing effort to individual species in a multi-species trawl fishery in northern Hecate Strait, British Columbia. All-species effort and individual species' landings are arranged by depth in selected area–time cells. In each area–time cell, each species is allotted the all-species effort expended in the depth intervals containing the rank-1 (most) and rank-2 (next-most) landings of that species. Comparison of the new option method with the conventional qualification method indicated that the latter method underestimated expended effort, particularly for less important species. Trends in effort and CPUE did not differ appreciably among methods. The new option method is deemed to be superior to the conventional qualification method.

Key words: effort allotment, multispecies trawl fishery, Hecate Strait, western Canada

WESTRHEIM, S. J. 1983. A new method for allotting effort to individual species in a mixed-species trawl fishery. Can. J. Fish. Aquat. Sci. 40: 352 – 360.

On trouvera dans l'article qui suit la description d'une nouvelle méthode pour attribuer l'effort de pêche à des espèces individuelles dans une pêche au chalut d'espèces multiples dans le nord du détroit d'Hecate, en Colombie-Britannique. L'effort dirigé sur toutes les espèces et les débarquements d'espèces individuelles sont disposés selon la profondeur dans des cellules superficie-temps. Dans chacune de ces cellules, on attribue aux espèces individuelles l'effort dirigé sur toutes les espèces dans les couches bathymétriques contenant les débarquements de rang 1 (les plus volumineux) et de rang 2 (les suivants) d'une espèce particulière. Si l'on compare cette nouvelle méthode avec la méthode conventionnelle de qualification, on constate que cette dernière sous-estime l'effort, en particulier dans le cas d'espèces de moindre importance. Les tendances de l'effort et des PUE ne diffèrent pas appréciablement dans les deux méthodes. On considère la nouvelle méthode comme étant supérieure à la méthode conventionnelle.

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ALLOTMENT of fishing effort to individual species in a mixed-species fishery has customarily been accomplished by establishing, usually arbitrarily, some qualification level (%) for catches deemed to be the result of targetted effort. That is, in any catch of mixed species, all the effort expended to produce the catch is allotted to each species whose contribution equals or exceeds the qualification percentage. Estimated total effort for each species is calculated by dividing the corresponding total catch by qualified CPUE (qualified catch ÷ qualified effort). Intuitively, this method seems fraught with hazards, both biological and economic. Where effort is considered to be an index of fishing mortality ($F = qf$) and CPUE is considered to be an index of abundance, each index should be derived independently. Economic factors may create variable demand for one or more of the individual species, such that catch limits are imposed intermittently. These individual limits may cause discard at sea of otherwise marketable fish. Such discards, if not reported, would affect estimates of both effort and CPUE.

A survey of the literature yielded few reports which deal with either methods, or evaluation thereof, for allotting fishing effort in a mixed-species fishery. In ICNAF/ICES/FAO[1] (1960), special attention was addressed to estimation of effort and CPUE for: (a) several species caught by the same gear; and (b) one species caught by several different gears. For multispecies fisheries, the report suggested three methods for allotting effort: (1) detailed subdivision by time and place to isolate effort on each species; (2) frequency–distribution of proportions for each species to isolate species accounting for a large proportion of catches; and (3) establishing maximum and minimum estimates of CPUE and effort to indicate range of actual values. None of these had been used. Interestingly, the report noted that: "Both bias and variation in effort and

[1]ICNAF = International Commission for the Northwest Atlantic Fisheries; ICES = International Council for the Exploration of the Sea; FAO = Food and Agricultural Organization of the United Nations.

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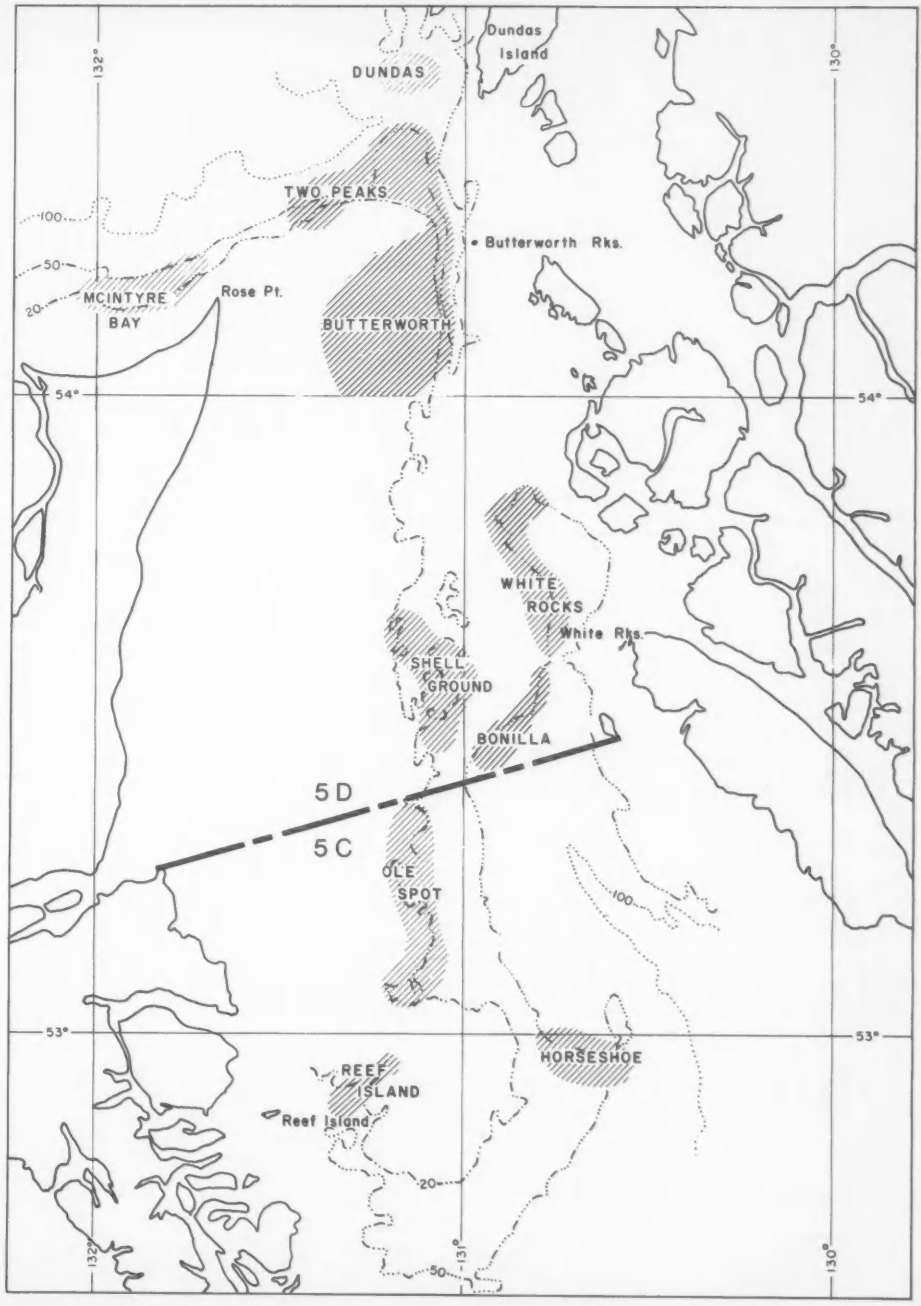

FIG. 1. Trawling grounds in Hecate Strait, British Columbia. Dotted lines are depth contours in fathoms.

TABLE 1. Mean landing statistics for selected species from Two Peaks and Butterworth grounds, April–June and July–September, 1958–78. (Percentages in parentheses.)

	Two Peaks		Butterworth		
	April–June	July–Sept.	April–June	July–Sept.	Total
Effort (h)					
All-species	616	797	717	286	2416
Landings (t)					
All-species	500	1261	528	311	2600 (100)
	(19)	(49)	(20)	(12)	(100)
Pacific cod	254	730	141	83	1208 (46)
	(21)	(60)	(12)	(7)	(100)
Rock sole	27	179	153	151	510 (20)
	(5)	(35)	(30)	(30)	(100)
English sole	89	77	160	40	366 (14)
	(24)	(21)	(44)	(11)	(100)

catch-per-unit-effort indices are likely to be greater and more influenced by economic factors in a mixed fishery than in one for a single species." (ICNAF/ICES/FAO 1960, p. 13).

In Gulland (1964), emphasis was directed more towards factors affecting estimates of CPUE. However, in his Introduction he noted a number of unanswered questions, among which was "what is the best way to deal with catch-per-unit-effort data in mixed fisheries?" Hempel (1978) noted, for the North Sea fisheries, that there is "room for improvement, particularly in the correct allocation of effort to certain fish stocks."

Ketchen (1964) demonstrated, for a western Canadian mixed-species trawl fishery, the unfortunate consequences of using a constant qualification level for estimating CPUE and effort when the high-demand species studied underwent an uninterrupted and substantial decline in absolute abundance and relative importance in the landings. Sissenwine (1978) similarly noted, as a general case, that the qualification method leads to an inverse relationship between catchability coefficient and stock size, under the conditions noted by Ketchen (1964). Kimura (1981) remarked on the problem of which qualification level to select, and the hazard of using the qualification method in a mixed-species fishery.

This report describes a new method for allotting effort to individual species in a mixed-species trawl fishery off western Canada. Results are compared with those obtained using the conventional qualification method.

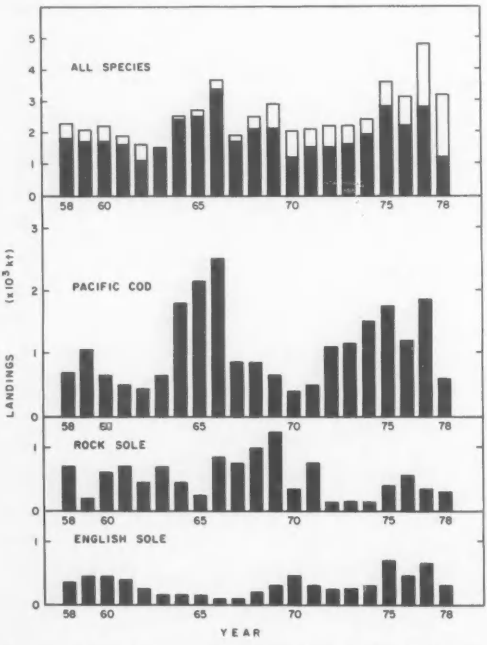

FIG. 2. Canada–U.S. trawl landings of all-species, Pacific cod, rock sole, and English sole from Two Peaks–Butterworth Ground, April–September, 1957–78. (Shaded area in all-species histograms = Pacific cod + rock sole + English sole.)

Materials and Methods

The multispecies fishery to which the new method was applied takes place during April–September on Two Peaks and Butterworth grounds in northern Hecate Strait (Fig. 1). The three principal species involved are Pacific cod (*Gadus macrocephalus*), rock sole (*Lepidopsetta bilineata*), and English sole (*Parophrys vetulus*). Together, they usually accounted for 70–98% of the all-species landings from Two Peaks–Butterworth Ground during April–September, 1958–78 (Fig. 2).

Only Canadian and United States vessels have participated in the trawl fishery of Hecate Strait. Detailed records (species, ground, depth) of landings[2] and effort are only available for Canadian vessels. However, the Canadian share of the landings has exceeded 70% since 1960, and has been virtually

[2]The term catch is conventionally, but at times inaccurately, used as a synonym for landing. In this trawl fishery some of the catch is discarded at sea (undersized or unsalable at the time), and rarely has an accurate record been maintained of this discard. The terms landing and LPUE (landings per unit effort) are used in this report in the interest of accuracy.

100% since 1971. Canadian and U.S. trawlers were comparable in size and gear.

Canada–U.S. trawl landings, by species and by month, were obtained from the Groundfish Data Series of the Pacific Marine Fisheries Commission (Portland, OR, U.S.A.). These data are recorded by international statistical area. Two Peaks–Butterworth Ground lies in Area 5D.

Canadian landing statistics are collected in detail by port liaison officers who interview trawl captains at the time of landing. Information collected includes, for each ground trawled, depth range(s) (fath) trawled, hours and days trawled, and landings (weight) by species. These records are stored on computer tapes at the Pacific Biological Station (Nanaimo, B.C.). For this analysis, depth trawled is the midpoint of the depth range reported. Proportion of Canadian landings from Hecate Strait, for which there was matching interview data, has been variable, but rarely less than 70% per annum, by weight.

Four area–time cells were selected for analysis — Two Peaks/Quarters II (April–June) and III (July–September); and Butterworth/Quarters II and III. Two Peaks Ground has a total area of 138.3 square nautical miles (474 km^2) over the depth range of 10–79 fath (18–145 m), and the surficial sediment is sand. Butterworth Ground has a total area of 229.5 square nautical miles (787 km^2) over a depth range of 10–69 fath (18–126 m). Surficial sediments are sand or sand and gravel. Negligible trawling occurs on either ground at depths shallower than 10 fath. Following is a summary of the areas by 10-fath interval:

Depth interval (fath)[a]	% area (square nautical miles)[b]	
	Two Peaks	Butterworth
10–19	21.5	76.0
20–29	9.5	2.5
30–39	19.4	3.8
40–49	18.3	7.7
50–59	12.1	8.4
60–69	10.2	1.6
70–79	9.1	—
Total	100.1 (138.3)	100.0 (229.5)

[a]1 fathom = 1.83 m.
[b]1 nautical mile = 1852 m.

Quarters II and III were selected for analysis because most of the annual landings occur at that time. Mean proportions of annual landings during Quarters II and III were 84% for Pacific cod, 90% for rock sole, and 70% for English sole.

Detailed records of effort and landings by ground, quarter-year, and 10-fath depth interval were reported by Westrheim et al. (1981).

Option Method

Allotment of trawling effort involves five steps: (1) calculate all-species effort in each area–time–depth cell (ground/quarter-year/10-fath depth interval); (2) calculate landings for each species in each area–time–depth cell; (3) for each species in each area–time cell, determine depth intervals for rank-1[3] and rank-2[3] landings; (4) allot all-species effort from depth intervals containing rank-1 and rank-2 landings to species in question (= option-2 effort); and (5) extrapolate option-2 effort to total effort. Algebraic details are shown in the Appendix.

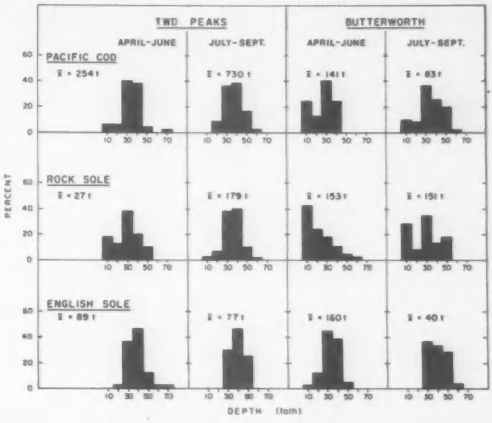

FIG. 3. Depth distribution (fath) of rank-1 + rank-2 landings of Pacific cod, rock sole, and English sole from Two Peaks and Butterworth grounds during April–June and July–September 1958–78.

Qualification Method

Qualification method for allotting effort does not directly involve depth of capture. Qualification level is 25% for each of the three species. That is, total interviewed effort for an individual trip, or identifiable portion thereof, is allotted to each species accounting for at least 25% of the landing in question. LPUE equals qualified landings divided by qualified effort. Total effort equals total landing divided by LPUE.

Results

During April–September 1958–78, Canada–U.S. all-species landings from Two Peaks–Butterworth Ground averaged 2600 t per annum, and effort, 2416 h (Table 1). Pacific cod landings accounted for 46%; rock sole, 20%; and English sole, 14%. Principal area–time cells were Two Peaks/Quarter III for Pacific cod and rock sole, and Butterworth/Quarter II for English sole (44%).

Depth distribution of annual rank-1 and rank-2 landings varied among species and area–time cells (Fig. 3). Pacific cod and English sole depths were primarily 30–39 and

[3]Rank-1 landing = largest landing among depth intervals of an area–time cell. Rank-2 landing = next-largest landing among depth intervals in the same area–time cell.

TABLE 2. Depth distribution (fath), by month, of Canada interviewed all-species effort (h) and landings (kg) of Pacific cod, rock sole, and English sole, Butterworth Ground, April–June, 1977.[a]

Depth interval (fath)	Month				Month				Month			
	April	May	June	Total	April	May	June	Total	April	May	June	Total
	All-species (h)				*Pacific cod (kg)*				*Rock sole (kg)*			
10–19	68	161	110	339	13 013	44 889	27 783	85 685	6568	19 397	14 652	40 617
20–29	—	59	28	87	—	6 059	1 251	7 310	—	6 506	7 845	14 351
30–39	62	217	98	377	26 273	21 871	10 994	59 138	630	9 350	23 490	33 470
40–49	50	113	104	267	2 091	9 323	10 284	21 698	1000	196	6 989	8 185
50–59	—	1	14	15	—	—	1 274	1 274	—	—	3 862	3 862
60–69	—	—	15	15	—	—	150	150	—	—	39	59
Total	180	551	369	1100	41 377	82 142	51 736	175 255	8198	35 449	56 897	100 544

Depth interval (fath)	Month				Month			
	April	May	June	Total	April	May	June	Total
	English sole (kg)							
10–19	—	1 727	13 910	15 637				
20–29	—	8 235	388	8 623				
30–39	3734	72 096	40 709	116 539				
40–49	2758	38 159	35 470	76 387				
50–59	—	485	5 427	5 912				
60–69	—	—	2 333	2 333				
Total	6492	120 701	98 238	225 431				

[a]Canada–U.S. All-species trawl landings from Area 5D, April–June 1977 = 2384 t. Canada interviewed all-species trawl landings from Area 5D, April–June 1977 = 2069 t.

40–49 fath, although in some years, Pacific cod was prominent in 10–19 fath, particularly during April–June on Butterworth Ground. Rock sole displayed greater diversity in depth distribution. Principal depths were 10–19 fath (all area–time cells except Two Peaks/Qtr. III); 40–49 fath and/or 30–39 fath (all area–time cells except Butterworth/Qtr. II); and 50–59 fath (Butterworth/Qtr. III).

OPTION-2 METHOD

An example of the computations involved in the Option-2 method (and alternative options 1 and 3)[4] is provided using the area–time cell of Butterworth/April–June 1977. First, interviewed Canadian all-species effort, and landings by species, are arranged by month and 10-fath depth interval, and summed by quarter year (Table 2).[5] Then the quarter-year arrays were extrapolated to total Canada–U.S. all-species effort, and landings by species (Table 3). Canada–U.S. all-species landing from Area 5D for April–June 1977 was 2384 t, and Canada interviewed all-species landing for the same area–time cell was 2069 t. Thus, the extrapolation ratio was 2384/2069. Corresponding extrapolation ratios for individual species were 632/561 for Pacific cod, 220/212 for rock sole, and 440/396 for English sole. Results of the mini-analysis were that among-method landings utilization (as a percent of total landings) increased from 40–51% for Option-1 to 88–95% for Option-3; and so in general did estimated total effort, 792–975 h for Option-1 method and 1056–1232 h for Option-3 method.

Principal area–time cells for each species were selected for analysis employing options 1, 2, and 3 for the period 1958–78 (Table 4). Results were similar to those obtained for Butterworth/April–June 1977. Landings utilization proportion among species was 55–68% for Option 1, 82–89% for Option 2, and 94–97% for Option 3. Calculated total effort for Option 2 was 143–160% of Option-1, and Option-3 effort was 181–198% of Option 1. There was no difference in time–series trends among methods.

A second Option-2 analysis was undertaken which eliminated the minor area–time cells for each species (see Table 1) — Butterworth/Qtr. III for Pacific cod and English sole; and Two Peaks/Qtr. II for rock sole. Only minor changes in calculated effort resulted (+2% for Pacific cod; −10% for rock sole; and +1% for English sole).

Option-2 method was selected for two reasons. First, it utilized a substantial proportion (83–89%) of the total landings. Second, the probability of overestimating effort seemed, intuitively, to be less than that with the Option-3 method, particularly for rock sole.

OPTION-2 VS. 25% QUALIFICATION

Comparison of the two methods, as applied to each species,

[4]Option 1 = rank-1 landings; Option 2 = rank-1 + rank-2 landings; Option 3 = rank-1 + rank-2 + rank-3 landings.

[5]In this example, the near-equality of the rank-2 (10 994 kg) and rank-3 (10 284 kg) landings of Pacific cod in June suggests that a more flexible method for selecting key depth intervals would be desirable. However, in the quarter-year arrays, few examples of this phenomenon occurred (Westrheim et al. 1981).

TABLE 3. Landing statistics, by option, for selected species from Butterworth Ground, April–June, 1977.

Depth interval (fath)	All-species effort (h)	Landings (t)			
		Pacific cod	Rock sole	English sole	All-species
10–19	390	97(1)[a]	42(1)	17(3)	162
20–29	100	8	15(3)	10	44
30–39	435	67(2)	35(2)	128(1)	304
40–49	308	24(3)	9	85(2)	198
50–59	17	1	4	7	16
60–69	17	T	T	3	10
Total	1267	197	105	250	734

	Option 1 (Rank-1)	Option 2 (Rank 1+2)	Option 3 (Rank 1+2+3)
	Pacific cod		
Landings (t)	97(49)[b]	164(83)	188(95)
Effort (h)	390	825	1133
LPUE (kg/h)	249	199	166
Total effort (h)	792	991	1187
	Rock sole		
Landings (t)	42(40)	77(73)	92(88)
Effort (h)	390	825	925
LPUE (kg/h)	108	93	99
Total effort (h)	975	1125	1056
	English sole		
Landings (t)	128(51)	213(85)	230(92)
Effort (h)	435	743	1133
LPUE (kg/h)	294	287	203
Total effort (h)	850	872	1232

[a]Rank.
[b]Percentage of total landing.

TABLE 4. Mean landings (t) and effort (h), by option method, from selected area–time cells, for Pacific cod, rock sole, English sole, 1958–78.

Parameter	Total landing (t)	Option 1			Option 2			Option 3		
		Landing (t)	Effort (h)	Total effort[a] (h)	Landing (t)	Effort (h)	Total effort[a] (h)	Landing (t)	Effort (h)	Total effort[a] (h)
				Pacific cod (Two Peaks/Qtr III)						
$\bar{x}$	730	403	368	667	598	525	641	689	667	707
% total	—	55	—	—	82	—	—	94	—	—
% Opt.-1							96			106
				Rock sole (Two Peaks/Qtr III)						
$\bar{x}$	177	121	335	490	157	520	586	172	663	682
% total	—	68	—	—	89	—	—	97	—	—
% Opt.-1							120			139
				English sole (Butterworth/Qtr II)						
$\bar{x}$	130	72	213	385	114	340	388	126	405	418
% total	—	55	—	—	88	—	—	97	—	—
% Opt.-1							101			109

[a]Total effort = (total landing)(option effort)/(option landing).

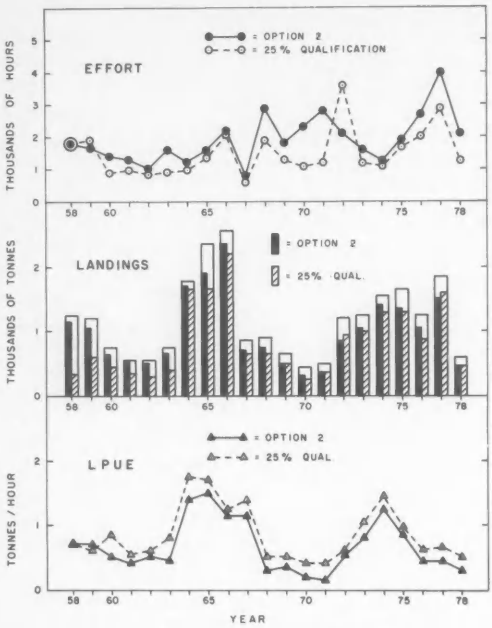

FIG. 4. Pacific cod landing statistics, by method, for Two Peaks–Butterworth Ground, April–September 1958–78.

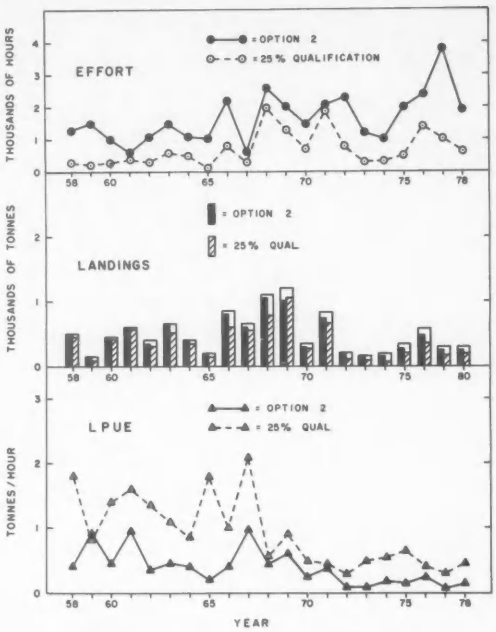

FIG. 5. Rock sole landing statistics, by method, for Two Peaks–Butterworth Ground, April–September 1958–78.

was based on the combined statistics of the four area–time cells for the period 1958–78.

For Pacific cod, trends and fluctuations in effort, landings, and LPUE were similar among methods (Fig. 4). On average, Option-2 effort values were larger; utilized landings were larger; and LPUEs were smaller. For LPUE, the relative range factor (maximum value ÷ minimum value) was larger, 8.8 vs. 4.6. This factor may reflect sensitivity to changes in abundance, i.e. values vary directly with sensitivity.

For rock sole, trends and fluctuations in effort, landings, and LPUEs were also similar among methods (Fig. 5). On average, Option-2 effort values were larger; utilized landings were larger; LPUEs were smaller; and the sensitivity factor was larger (12.3 vs. 7.6).

For English sole, trends and fluctuations in effort, landings, and LPUEs were also similar among methods (Fig. 6). On average, Option-2 effort values were larger; utilized landings were larger; LPUEs were smaller; and the sensitivity factor was larger (9.2 vs. 4.1).

In summary, in comparison with the 25% qualification method, the Option-2 method produced larger (and probably more realistic) estimates of total effort; utilized a larger proportion of the total landings; and yielded smaller, and possibly more sensitive estimates of LPUE. Time–series trends in effort and LPUE were similar. Interestingly, for rock sole, use of the 50% qualification level produced a smaller estimate for effort (−18%) and a larger estimate for LPUE (+28%) than those values obtained by the 25% qualification method. Utilized landings were also, of course, less for the 50% qualification method (−20%). Qualification-method estimates of effort expended for the minor species (rock sole and English sole) appear to be grossly in error.

Discussion

For mixed-species trawl fisheries, the option method for allotting effort to individual species has a number of advantages over the conventional qualification method. First, allotment is appropriate to all species in the fishery which are equally available to the gear utilized. Second, effort (but not LPUE) estimates are independent of intermittent market quotas imposed on individual species in the mixed-species fishery. Third, bathymetric arrays of effort and resulting landings expand the conception of the fishing activities, and may well provide new insights into the dynamics of the populations. For example, the option method emphasizes the amount of effort sustained communally by all susceptible species in an area–time cell, and de-emphasizes 'targetting,' which is usually an unrealistic concept when applied to individual species in a multispecies fishery.

The option method does not meet the desirable criterion of independent estimates of total effort and LPUE. However, the "arbitrary" choice of depth intervals (rank-1 and rank-2 landings) is at least dictated by the bathymetric distribution of the species, and is probably independent of the absolute abundance of the species. Such is not the case for the qualification method.

The current study does not deal with relative fishing power

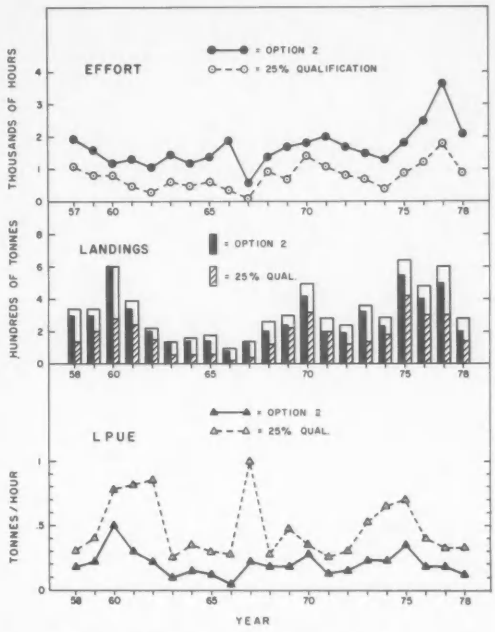

FIG. 6. English sole landing statistics, by method, for Two Peaks–Butterworth Ground, April–September 1958–78.

of the trawlers in the Canadian and U.S. fleets. Mean gross tonnage per Canadian vessel increased steadily during the study period, but most of the larger vessels concentrated on "volume" species such as rockfishes (Scorpaenidae). However, even if larger vessels trawled on Two Peaks–Butterworth Ground, their effort would be sustained by all species available in the depth intervals trawled.

Validity of the option method will be most dependent on equal temporal and spatial availability of all species to the fishing gear. For Two Peaks–Butterworth Ground, temporal and spatial demands were met for quarter-year and 10-fath depth interval units of time and space, respectively. Elimination of area–time cells contributing minor proportions of the total production of a species did not materially alter the landing statistics for that species. However, the data in Table 2 indicated availability (measured as kilograms or kilograms per hour) of the individual species was not equal among months within Quarter II. April accounted for only 12% of the quarterly landings of rock sole, and 4% of English sole. Elimination of April data reduced the total allotted effort by 23% for rock sole, and 22% for English sole. These are still relatively minor corrections compared to the +100% deviation from the estimates by the qualification method. Further refinements in the selection of area–time cells may become necessary for the individual case of Two Peaks–Butterworth Ground, but the option method appears to be superior to the qualification method for allotting effort to individual species in this mixed-species fishery.

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Appendix

Following are algebraic expressions of the five steps involved in allotting trawl effort to individual species in a multispecies trawl fishery:

Step 1 — Canada–U.S. all-species effort (E, in hours trawled), was calculated by ground by quarter year as follows:

$$\hat{E}_{ij} = \frac{L_i}{l_i}(e_{ij}),$$

where $\hat{E}_{ij}$ = Canada–U.S. all-species effort (h) in Area 5D (north Hecate Strait) for the ith quarter year and jth ground.

L_i = Canada–U.S. all-species landings[6] from Area 5D (north Hecate Strait) for the ith quarter year;

l_i = interviewed Canadian all-species landings[7] from Area 5D for the ith quarter year;

e_{ij} = interviewed Canadian all-species effort[7] in Area 5D for the ith quarter year and jth ground.

Each $\hat{E}_{ij}$ was distributed over the individual 10-fath depth intervals, in proportion to that of the corresponding e_{ij}.

[6]Includes midwater and on-bottom trawl landings (not separated in PMFC data). Midwater trawl is a negligible factor in the fishery for the three study species.

[7]Excludes midwater trawl landings.

Step 2 — Canada–U.S. landings of Pacific cod, rock sole, and English sole were each calculated as follows:

$$\hat{L}_{ij\text{A}} = \frac{L_{i\text{A}}}{l_{i\text{A}}}\, l_{ij\text{A}},$$

where $\hat{L}_{ij\text{A}}$ = Canada–U.S. landings of species A for the ith quarter year and jth ground;
$L_{i\text{A}}$ = Canada–U.S. landings of species A from Area 5D during ith quarter year;
$l_{i\text{A}}$ = interviewed Canadian landings of species A from Area 5D during the ith quarter year;
$l_{ij\text{A}}$ = interviewed Canadian landings of species A during ith quarter year from jth ground.

Similarly, each $\hat{L}_{ij\text{A}}$ was distributed over individual 10-fath depth intervals, in proportion to that of the corresponding $l_{ij\text{A}}$.

Steps 3 and 4 — Option-2 landings ($\hat{l}_{ij\text{A}}$) of species A for each area–time cell is the sum of the rank-1 and rank-2 Canada–U.S. landings among 10-fath depth intervals. Option-2 effort ($e'_{ij\text{A}}$) for species A for each area–time cell is the sum of the hours in the 10-fath depth intervals containing rank-1 and rank-2 landings of species A.

Step 5 — Canada–U.S. total allotted effort ($\hat{E}_{ij\text{A}}$) for species A, in area–time cell ij is calculated as follows:

$$\hat{E}_{ij\text{A}} = \frac{\hat{L}_{ij\text{A}}}{l'_{ij\text{A}}}\,(e'_{ij\text{A}}),$$

where $\hat{L}_{ij\text{A}}$ = Canada–U.S. total landings of species A in area–time cell ij.
$l'_{ij\text{A}}$ = Canada–U.S. option-2 landings of species A in area–time cell ij.
$e'_{ij\text{A}}$ = Canada–U.S. option-2 effort for species A in area–time cell ij.

Identification of Marine Fish Eggs: A Biochemical Genetics Approach[1,2]

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MORK, J., P. SOLEMDAL, AND G. SUNDNES. 1983. Identification of marine fish eggs: A biochemical genetics approach. Can. J. Fish. Aquat. Sci. 40: 361–369.

We studied inter- and intra-specific variation at LDH (lactate dehydrogenase; EC 1.1.1.27) loci in 11 gadoid and 6 flatfish species regularly occurring in Norwegian coastal waters by means of isoelectric focusing and histochemical staining techniques. No two species showed identical locus *A* (white skeletal muscle predominating) zymograms. Polymorphism at *LDH A* was observed in haddock (*Gadus aeglefinus*), coalfish (*G. virens*), Norway pout (*G. esmarkii*), four-bearded rockling (*Onos cimbrius*), and dab (*Limanda limanda*). The allelic nature of observed LDH variants was confirmed by controlled crossings in cod (*G. morhua*, locus *B*), Norway pout (locus *A*), and haddock (locus *A*). Analyses of artificially fertilized eggs (in four species) and prenatal eggs from ripening ovaries (in 10 species) revealed a general predominance of locus *A* products. The maternal LDH A activity present in newly released eggs was overtaken by embryo-synthesized enzyme 1–2 d after fertilization. No unique embryonic LDH loci were observed. LDH A zymograms thus appear to be useful as a practically diagnostic tool for the identification of the pelagic fish eggs usually found in these waters. The identification method, applied to samples of pelagic eggs collected at the coast of northern Norway during March–May 1981 and 1982, showed that in a total of ~1500 eggs, the following species were represented: cod, Norway pout, haddock, coalfish, dab, plaice (*Pleuronectes platessa*), and long rough dab (*Hippoglossoides platessoides*). The species composition in these egg samples varied considerably with sampling location and sampling depth.

Key words: fish egg identification, biochemical genetics, tissue enzymes, gadoids, flatfishes

MORK, J., P. SOLEMDAL, AND G. SUNDNES. 1983. Identification of marine fish eggs: A biochemical genetics approach. Can. J. Fish. Aquat. Sci. 40: 361–369.

Nous avons étudié la variation inter et intraspécifique aux loci de LDH (lactate déshydrogénase; EC 1.1.1.27) chez 11 espèces de gadoïdes et 6 de poissons plats régulièrement trouvés dans les eaux côtières de la Norvège, utilisant à cette fin des méthodes de focalisation isoélectrique et de coloration histochimiques. Les zymogrammes du locus *A* (en grande partie du muscle squelettique blanc) diffèrent d'une espèce à l'autre. On observe un polymorphisme à *LDH A* chez l'aiglefin (*Gadus aeglefinus*), le lieu noir (*G. virens*), le tacaud norvégien (*G. esmarkii*), la motelle à quatre barbillons (*Onos cimbrius*) et la limande (*Limanda limanda*). La nature allélique des variants de LDH observés est confirmée par des croisements contrôlés chez la morue (*G. morhua*, locus *B*), le tacaud norvégien (locus *A*) et l'aiglefin (locus *A*). Des analyses d'oeufs fécondés artificiellement (de quatre espèces) et d'oeufs prélevés avant la ponte sur des ovaires en voie de maturation (de 10 espèces) montrent une prédominance générale de produits du locus *A*. L'activité de LDH A maternelle présente dans des oeufs nouvellement expulsés est remplacée par un enzyme synthétisé par l'embryon de 1 à 2 jours après la fécondation. Nous n'observons aucun locus de LDH embryonnaire unique. Les zymogrammes de LDH A semblent donc une méthode utile et pratique pour l'identification

[1]Contribution No. 208, Biological Station, Trondheim, Norway.
[2]Not all common and scientific names here conform to the AFS list.

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des oeufs de poissons pélagiques généralement trouvés dans ces eaux. Cette méthode d'identification a été appliquée à des échantillons d'oeufs pélagiques recueillis le long de la côte de la Norvège septentrionale entre mars et mai 1981 et 1982. On constate que, sur un total d'environ 1 500 oeufs, les espèces suivantes sont représentées : morue, tacaud norvégien, aiglefin, lieu noir, limande, carrelet (*Pleuronectes platessa*) et balai (*Hippoglossoides platessoides*). La composition par espèce de ces échantillons d'oeufs varie considérablement selon le site et la profondeur de l'échantillonnage.

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MANY marine fish species, e.g. all gadoids in Norwegian coastal waters, produce eggs that are pelagic after fertilization. The spawning of these species may overlap in both time and space; hence their eggs occur simultaneously in plankton samples. Frequently these eggs possess species-specific traits which permit visual identification. Keys for such identification have been constructed, based on characteristics such as color, shape, texture, number and size of oil globules, egg diameter, and embryo pigmentation (see e.g. Russel 1976 and references therein). In practice, egg diameter has been the only characteristic available for the discrimination between early stage eggs from several gadoids and flatfishes in Norwegian waters. This characteristic varies within species, and the egg size distributions show considerable overlapping between species (Fig. 1). For instance, the egg size 1.2 mm is shared by at least eight different species which all occur regularly in Norwegian coastal waters (cod, haddock, whiting, poutassou, pollack, coalfish, lemon sole, and witch).[3] Accordingly, varying proportions of the eggs in plankton samples may be unidentified or incorrectly identified. In fact, the discrimination between eggs from cod and haddock in Norwegian waters is even more problematic than indicated by Fig. 1; in these areas the egg diameter distribution for cod (1.20–1.63 mm; Solemdal and Sundby 1981) and haddock (1.12–1.65 mm; E. Moksness, State Biological Station, Flödevigen, personal communication) in practice prevents visual identifications until just prior to hatching, when the embryo has developed characteristic pigmentation.

The uncertainty regarding the identity of early stage eggs has for a long time affected the value of egg surveys in the Lofoten area (area A, Fig. 2), where ripe haddock occurs together with Arcto-Norwegian cod ("skrei") during spawning. Further, investigations of the spawning off Lofoten and the corresponding egg drift along the continental edge in area B (Fig. 2) have shown a mixture of cod and haddock eggs in the samples (visual identifications of late development stage eggs). Because of the considerable amounts of early stage eggs in these samples, the actual proportions of cod and haddock eggs have been unknown (Wiborg 1960). The geographical distribution of this egg concentration is distinct and clearly westward to the main track of skrei eggs from the Lofoten spawning. These eggs contribute a significant part to the pelagic eggs in area B (Fig. 2), but the lack of information on their actual species composition has hitherto prevented a closer evaluation of their significance in relation to skrei egg surveys.

Problems like these call for more efficient methods for fish egg identification. The purpose of the present study was to develop methods for biochemical genetics discrimination between pelagic fish eggs, with special reference to the early development stage eggs of cod and haddock, and to apply these methods during annual routine egg surveys in and north of the main spawning area of the Arcto-Norwegian cod stock in Lofoten, northern Norway (Fig. 2).

Material and Methods

Pelagic eggs were sampled with Juday nets and plankton pumps during March–May 1981 and 1982 on and north of the main spawning grounds of the Arcto-Norwegian cod stock (in this report referred to as "skrei" to distinguish it from Norwegian coastal cod, which spawns simultaneously in the same areas) in the Lofoten area (Fig. 2). Samples of the fish species present in these areas in the same periods were obtained by shrimp trawl (cod, haddock, coalfish, and Norway pout). Additional species (ripe specimens) were sampled by shrimp trawl in the Trondheimsfjord (Fig. 2) during March–May 1980, 1981, and 1982. A total of 17 species, including 11 gadoids and 6 flatfishes, were collected (Table 1).

Artificial fertilization with subsequent analyses of single egg isozyme patterns were performed for cod, haddock, Norway pout, and plaice. In each experiment, six different pairs of parents were used. Eggs and larvae were collected at various times after fertilization for enzyme analyses; in all species the first batch was collected after 8 h but subsequent sampling intervals were irregular and varied between species. Thus, in Norway pout and cod the second sample was collected by 10 h (Norway pout) and 36 h (cod), whereas in haddock and plaice the second egg batch was collected by 72 h after fertilization. The incubation temperature was 6°C for cod, haddock, and plaice, and 3°C for Norway pout eggs. Pending enzyme analyses, eggs were stored in liquid nitrogen or in a deep-freezer (−76°C).

Samples of heart, liver, and skeletal muscle tissues from adult fish (and for some species eggs from ripening ovaries) were cut out and frozen (liquid nitrogen) within 2 h after capture. They were subsequently stored at −76°C until analyzed.

Single eggs were picked up with tweezers and transferred to 300-μL polyethylene centrifuge tubes which were immediately sealed and put in liquid nitrogen. Each tube contained 10–20 μL of homogenization liquid in which the egg was immersed.

During thawing, ~4 volumes of a 1% solution of the appropriate ampholyte was added to the tissue samples which then were macerated with a glass rod and subsequently centrifuged

[3]See Table 1 for scientific names.

TABLE 1. The gadoid and flatfish species investigated for muscle LDH patterns. Information regarding sample size within species and cases of observed genetic polymorphisms is given (No. of alleles includes both common and variant alleles).

Species	Number	Variants	No. of alleles
Gadoids			
Atlantic cod (*Gadus morhua*)	>100	No	
Haddock (*G. aeglefinus*)	>100	Yes	3
Pollack (*G. pollachius*)	1	No	
Coalfish (*G. virens*)	6	Yes	2
Whiting (*G. merlangus*)	>100	No	
Poutassou (*G. poutassou*)	2	No	
Norway pout (*G. esmarkii*)	>100	Yes	2
Poor-cod (*Trisopterus minutus*)	4	No	
Silvery cod (*Gadiculus thori*)	10	No	
Four-bearded rockling (*Onos cimbrius*)	20	Yes	2
Tusk (*Brosme brosme*)	1	No	
Flatfishes			
Plaice (*Pleuronectes platessa*)	>100	No	
Flounder (*Platichtys flesus*)	5	No	
Dab (*Limanda limanda*)	1	Yes	2
Long rough dab (*Hippoglossoides platessoides*)	8	No	
Lemon sole (*Microstomus kitt*)	2	No	
Witch (*Glyptocephalus cynoglossus*)	16	No	

at 10 000 × *g* for 10 min (0°C) in a refrigerated centrifuge. The clear supernatant was used for enzyme analyses. Single fish eggs were processed in a similar fashion, except that the homogenization liquid had been added earlier (cf. preceding), and centrifugation was usually not performed.

ISOELECTRIC FOCUSING AND SPECIFIC ENZYME DETECTION

The equipment and experimental procedures were as described by Mork and Haug (1983). The focusing was performed using 0.7-mm-thick polyacrylamide gels, (T = 4.5%, C = 3%, Bis-crosslinked and photopolymerized) containing 1.8% Servalyte 4-9T as carrier ampholyte, on a modified Multiphor (LKB, Bromma, Sweden) apparatus. The gels were molded onto sheets of polyester film (Gel-Fix, Serva, Heidelberg). The electrical settings were 0.8 W/cm^2 gel, V_{max} = 1600 V. The anolyte used was 1 mol/L phosphoric acid and the catholyte 1 mol/L sodium hydroxide. The coolant was thermostated at 0°C and total focusing time was 2 h. On each gel which measured 235 × 100 mm, 50–100 individual protein extracts were run. The protein extracts were absorbed on pieces of filter paper and applied to the gel surface (usually 30–40 mm from the anode) after 15 min of prefocusing. The filter paper pieces were removed after 20 min further run.

After focusing, the gels for LDH staining were immersed in 0.5 mol/L pure Tris base containing (per 100 millilitres) DL-lactate (free acid): 1 mL, NAD: 10 mg, PES (phenazine ethosulfate): 5 mg, and NBT: 5 mg. Staining took place in the dark at 30°C and was usually sufficient after 2–5 min for adult tissues and 20 min for eggs. The reaction was stopped and excess staining reagents washed out of the gel (to prevent blue background) in water:ethanol:acetic acid (5:4:1). For the detection of SOD, the same procedure was followed, except that the reaction took place in daylight or, preferably, in a glass tray placed on a lightbox. The SOD patterns then appeared as uncolored zones against a bluish background, whereas the LDH zones could still be scored. The staining recipes for IDH, EST, and PGI[4] followed Allendorf et al. (1977), except for the use of higher pH in the IDH incubation bath (pure Tris base combined with PES) to speed up the reaction.

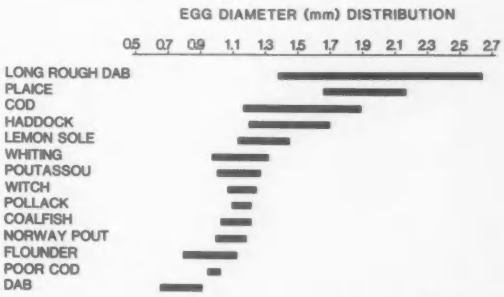

FIG. 1. Egg diameter distributions according to Russel (1976) in some commonly occurring gadoids and flatfishes in Norwegian waters. For visual egg identification purposes, Russel put these species in one group: "Spherical pelagic eggs with no oil globule and unsegmented yolk" where egg diameter is the discriminating characteristic. Note the considerable overlapping of this characteristic between species.

For storing and future reference, the washed gels were either completely dried onto the polyester support, or

[4]Abbreviations used: LDH = lactate dehydrogenase (EC 1.1.1.27), IDH = isocitrate dehydrogenase (EC 1.1.1.42), SOD = superoxide dismutase (EC 1.15.1.1), PGI = glucosephosphate isomerase (EC 5.3.1.9), and EST = nonspecific esterase.

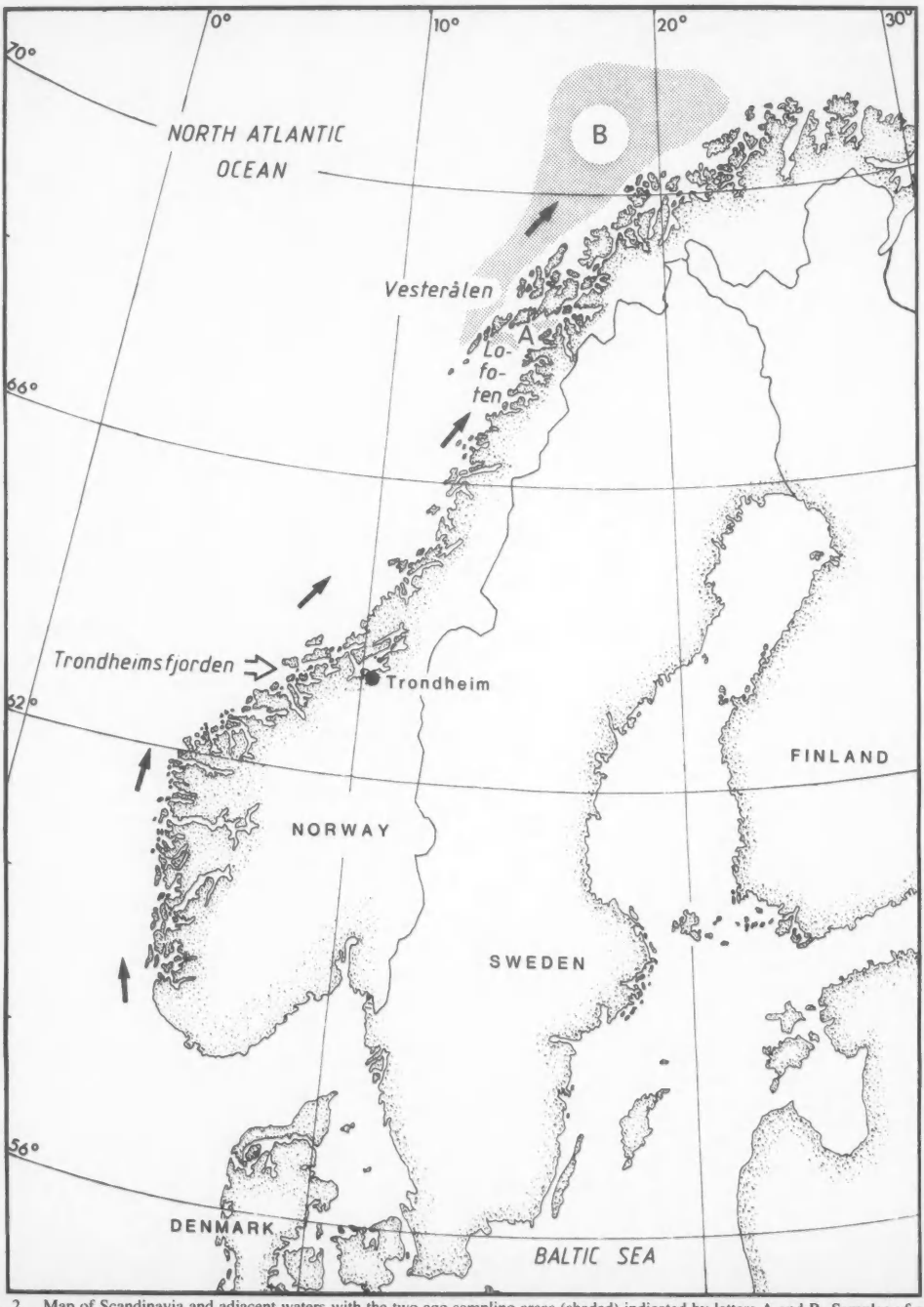

FIG. 2. Map of Scandinavia and adjacent waters with the two egg sampling areas (shaded) indicated by letters A and B. Samples of adult fish were collected in Lofoten and in the Trondheimsfjord. The Norwegian Coastal Current is indicated by black arrows.

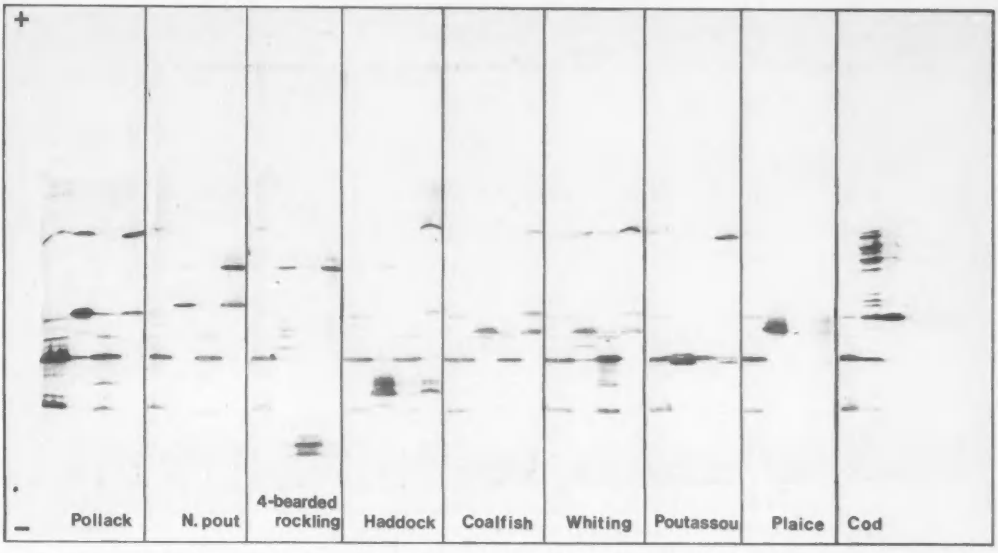

FIG. 3. Photograph of an isoelectric focusing gel (anode at the top) after staining for LDH, showing observed isozyme patterns in different tissue types in some common Norwegian gadoids plus plaice. Cod liver extract was used as an internal control on the gel and applied at the left of each cell. From left to right, the other patterns in each cell are produced by skeletal muscle, liver, and heart extracts from each species. In the right-most cell (cod), the order of tissues is somewhat different (from left: liver, heart, and skeletal muscle). Note the extensive interspecific variation in skeletal muscle band positions as compared to the more similar positions of liver and heart bands.

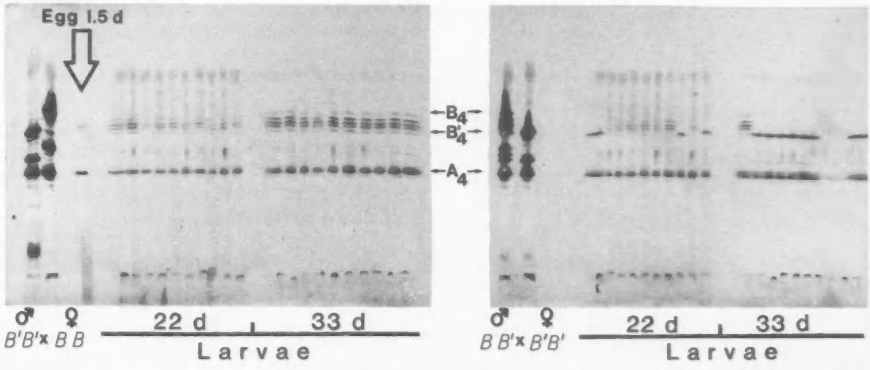

FIG. 4. LDH zymograms produced by parents and offspring (individual eggs and larvae) in two crossings of cod. The parental genotypes at the polymorphic locus *B* (heart predominating in cod) are given (cf. text for nomenclature). The gel positions of the homotetrameric isozymes with subunit types A, B′, and B are indicated. Products from the paternal allele at *LDH B* could be detected 1.5 d after fertilization (arrow). Note the genotypic proportions among the offspring which confirm the hereditability of LDH characteristics at the *B* locus.

alternatively, partly dried and overlayed with another polyester film sheet.

The LDH patterns produced by single eggs were compared to those produced by standard samples (adult tissues or egg samples from various species) run on the same gel.

The term locus *A*, as used in this report, refers to the locus which controls the synthesis of subunits for the white skeletal muscle predominating form (the A tetramer) of LDH. Although one may seem to be on safe empiric ground with this designation (see e.g. Markert and Holmes 1969, and references therein), it should be noted that for several species in our repertory, no immunochemical or kinetic evidence is available which confirms the evolutionary homology of the LDH molecules we have called A tetramers.

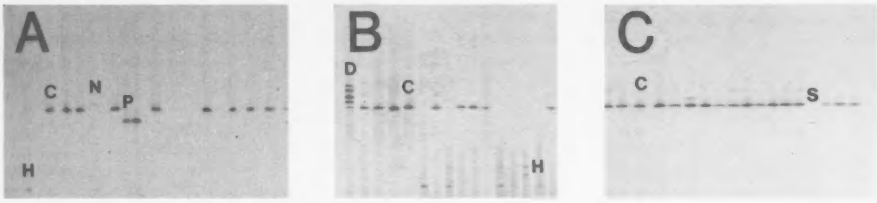

FIG. 5. Appearance of LDH patterns after isoelectric focusing of extracts from single eggs from various fish species (anode at the top). Species code: H = haddock, C = cod, N = Norway pout, P = plaice, D = dab, and S = coalfish. Photograph A: Zymograms from eggs of known origin (the eggs were sampled 8 h after artificial fertilizations). Photographs B and C: Some of the patterns observed during routine analyses of egg samples from the Lofoten and Vesterålen areas.

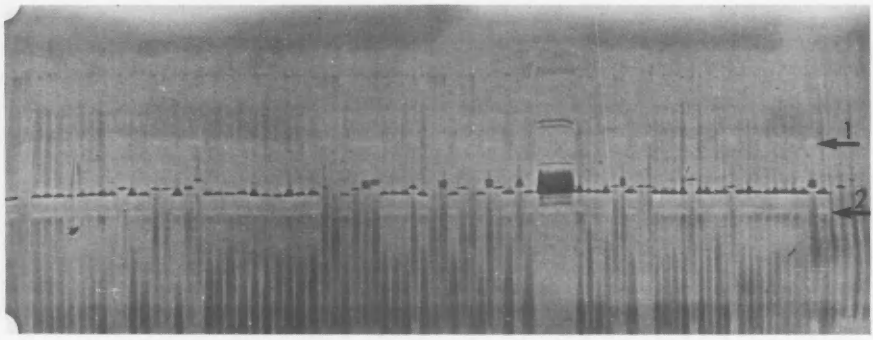

FIG. 6. Routine LDH zymogram (anode at the top) of single pelagic eggs from the Lofoten area. This sample contained only cod and Norway pout eggs. The two-allele polymorphism at the *A* locus in the latter (cf. Table 1 and Fig. 7) is manifested by three genotypes which bands are seen anodal to the predominating band in extracts from cod eggs. The broadbanded pattern is produced by adult cod skeletal muscle extract. This gel was stained in daylight to visualize zones of SOD activity. Note the different positions of SOD zones in Norway pout (arrow 1) and cod (arrow 2) eggs.

Results and Discussion

OBSERVATIONS FROM LDH ZYMOGRAMS

Staining for LDH revealed distinct zones of activity in all the investigated tissue types in all species. Tissue characteristic isozymes were observed (Fig. 3). Although the 11 gadoids and 6 flatfishes include taxonomically closely related groups, no two species displayed identical LDH A patterns. This result might, provided genetic control of the observed LDH A variation and the recognizable expression of this locus in eggs, be used for egg identification purposes.

Analyses of offspring from the artificial fertilizations provided direct confirmation of the allelic nature of the observed LDH variants in cod, haddock, and Norway pout. In these species, which are polymorphic for their *B*, *A*, and *A* loci of LDH, respectively, various genotypic combinations of parents were chosen for this purpose. Subsequent analyses of LDH in single eggs and larvae from these crossings revealed isozyme patterns and genotypic proportions in accordance with the expectations for simple Mendelian inheritance of genes coding for subunits of a tetrameric protein. Figure 4 shows some results from such experiments in cod (the parental *LDH B* genotype designation refers to the nomenclature of Odense et al. 1969, adopted by Mork et al. 1980 for cod in these areas). We have no reason to doubt that also for the other species in Table 1, observed LDH A patterns represent reliable, inherited characteristics which may be used for species identification purposes.

In the artificially fertilized eggs from cod, haddock, Norway pout, and plaice, LDH A tetramer activity was predominant in the early stages (Fig. 5A). Also in "wild" eggs visually identified as belonging to long rough dab (cf. Fig. 1), the egg LDH band corresponded to the LDH A isozyme in adult specimens. In late stage eggs from the artificial fertilizations, additional loci could be expressed, but in all cases the egg isozymes corresponded to patterns observed in adult fish tissues. Thus, in cod, haddock, Norway pout, and plaice, no unique embryonic LDH locus was expressed.

Analyses of single prenatal eggs from ripe or ripening ovaries in various species (cod, Norway pout, coalfish, whiting, four-bearded rockling, poor-cod, silvery cod, lemon sole, long rough dab, dab, and flounder) showed the A tetramer activity to be predominant. As for the origin of the LDH molecules active in newly fertilized eggs, some information was obtained from artificially fertilized eggs from cod, Norway pout, and haddock: paternal alleles were not expressed 8 h after fertilization but were detected after 72 h in all three

species. In cod, the paternal allele at the polymorphic *B* locus was scorable in single eggs 36 h after fertilization (6°C, Fig. 4), indicating that the embryonic LDH synthesis must have started at an earlier stage. On the other hand, in Norway pout eggs incubated at 3°C the paternal allele at the polymorphic locus *A* was not expressed by 10 h. If inter-specific and inter-locus variation may be neglected, then these results suggest that at an age of 1–2 d, presumably somewhat dependent upon temperature, the embryonic LDH synthesis overtakes the maternal activity present in the eggs. However, because A tetramer activity is predominant in both unfertilized and fertilized eggs, its suitability for identification purposes is unaffected.

From our experimental results it thus appears that the LDH A isozymes may be expected to predominate in early stage eggs from the various species, and thus provide a basis for species identification. This expectation has been confirmed in all cases where a control was possible. Also, the actual LDH patterns observed in routine analyses of pelagic eggs (Fig. 5B, C, and Fig. 6) always corresponded perfectly to the LDH A pattern in one or another of the species in Table 1. The LDH A patterns observed in each of these 17 species have been compiled in Fig. 7, in which the most significant bands of activity have been drawn; i.e. the patterns we expect to observe by analyses of eggs from the various species. According to our genetic interpretations, these patterns are produced by proteins coded for by alleles at one locus (locus *A*) in each species. As concerns the dab LDH zymogram, this interpretation is provisional; the observed pattern (Fig. 5C and Fig. 7) may either represent a heterozygote at locus *A*, or alternatively be produced by proteins coded for at two loci, equally expressed in white skeletal muscle and, evidently, also in eggs. Because only one adult specimen has been analyzed, this question cannot be settled at present. Pending further analyses, we have chosen the first interpretation (cf. Table 1).

Polymorphism at the *A* locus was observed in several species (Table 1 and Fig. 7). The observed variant patterns did not affect the diagnosticity of *LDH A*. However, possibly additional polymorphisms may be found in species where only one or a few adult specimens have been analyzed. These may interfere with banding interpretations and could result in some mistaken identifications. Also, the present species repertory is not quite complete for application in Norwegian coastal waters; e.g. gadoids such as ling (*Molva molva*) and bib (*Trisopterus luscus*) and various rocklings and flatfishes have yet not been investigated.

Nevertheless, the LDH A characteristics seem promising as a practically diagnostic key to the identification of early development stage pelagic eggs in the investigated waters, and the discrimination between eggs from cod and haddock (the primary focus of this study) is very easily performed with our method. The LDH A band in cod eggs was distinct and invariable. Because cod eggs predominated in most of our samples, their easily recognized LDH zymograms in practice acted as internal control bands on the gels. In haddock, the homotetrameric products coded for by the most commonly observed *LDH A* allele (frequency 0.9 in the present egg samples) displayed by far the most cathodic bands of activity among the investigated species and were thus readily recognized on the gels (Fig. 5A, B, and Fig. 7), as also were the corresponding heterozygous patterns (Fig. 5B and Fig. 7). We observed no homozygotes for variant alleles at *LDH A* in 63 haddock eggs, but did not expect so, either, from the actual

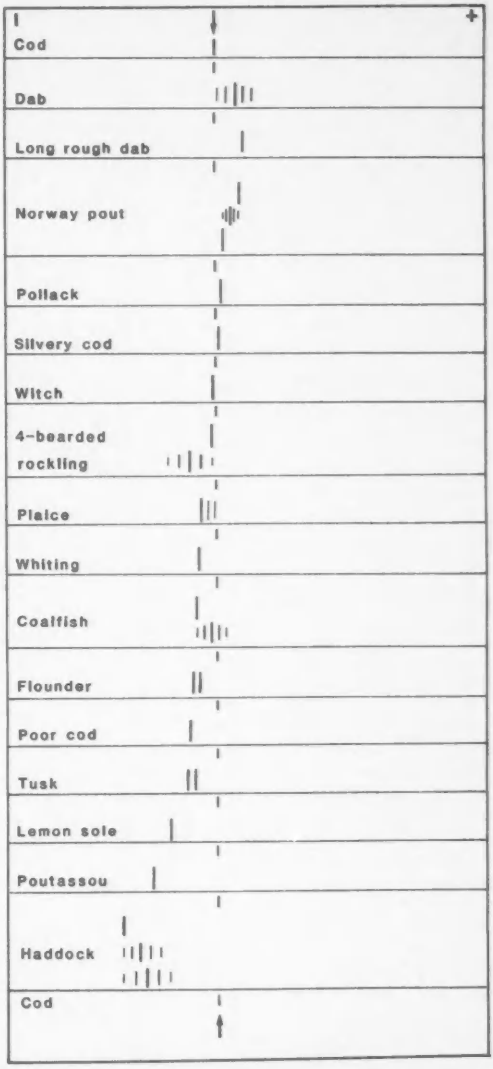

FIG. 7. Compiled results from observations on LDH A patterns in muscle extracts from 11 gadoids and 6 flatfishes from Norwegian coastal waters (anode at the top). For comparison, the cod locus *A* band (arrows) was drawn at the left of each cell. In tusk, flounder, and plaice, the extra bands are believed to be anodally positioned satellites. Five-banded patterns represent heterozygotes at the *A* locus.

TABLE 2. Compiled results from biochemical genetics identification of pelagic fish eggs in 1981 and 1982. See Fig. 2 for location code.

		Number of eggs from different species							
Date	Location	Cod	Haddock	Norway pout	Coalfish	Plaice	Dab	Long rough dab	*n*
March 25, 1981	A	177	0	27	14	3	0	0	221
May 5, 1981	B	178	36	1	0	10	0	0	225
Apr. 4, 1982	A	490	0	228	2	2	0	1	723
Apr. 20, 1982	B	228	8	0	5	3	0	0	244
May 10, 1982	B	82	17	0	1	0	1	0	101

TABLE 3. Observed species composition in egg samples from various depths. The samples were taken on skrei spawning grounds in area A (Fig. 2) on April 4, 1982. (No haddock or dab eggs were found).

	Number of eggs from different species					
Depth (m)	Cod	Norway pout	Coalfish	Plaice	Long rough dab	*n*
0–10	232	0	2	0	0	234
30	87	13	0	0	0	100
40–60	90	64	0	1	1	156
70	6	44	0	0	0	50
90	16	34	0	0	0	50
100	6	43	0	1	0	50
110	31	19	0	0	0	50
120	22	11	0	0	0	33

variant allele frequencies. Frequently, in our egg samples, one or two species predominated (e.g. cod and haddock or cod and Norway pout), and the repetitive occurrence of identical LDH patterns on the gels facilitated comparisons and made the identifications very straightforward (see, e.g. Fig. 6).

In general, we recommend use of only part of the individual egg extract in routine analyses. If a second run is necessary to distinguish between closely positioned bands, spare extracts from the actual samples should be applied side by side on the same gel. In our experience, the differences in pI of LDH A bands are sufficient to allow identification with this procedure. Although we have not experienced such a situation, some species may display identical LDH A zymograms. In such situations the first step would be to stain for SOD, as this can be performed on the same gel without addition of chemicals and without additional formazan bands interfering with the LDH patterns (cf. Fig. 6). If this is not sufficient for identification, probably a range of other enzymes in eggs may be visualized. With strict sample economy and generosity of substrate and cofactor concentrations in the staining solutions, we have been able to score LDH, SOD, IDH, EST, and PGI in individual cod eggs. Of course, a visual inspection of eggs prior to the biochemical analyses will always delimit the range of possible species and in most cases probably make multilocus or multienzyme approaches unnecessary.

RESULTS APPLYING THE METHODS DESCRIBED

During 1981 and 1982, a total of ~1500 pelagic eggs from Lofoten and Vesterålen were biochemically identified. As expected, the main part of the eggs in these areas was from cod. As revealed by visual inspection, and also by the LDH loci expression, cod eggs collected in area B were on average older than those from area A. Generally, cod eggs in these more northern areas are believed to stem mainly from the skrei spawning in area A, but also partly from cod spawnings further south on the coast of Norway. In order of their frequency of occurrence, the following additional species were represented by their eggs: Norway pout, haddock, coalfish, plaice, dab, and long rough dab (Table 2).

Typically, both in 1981 and 1982, the proportion of non-cod eggs in area A increased with depth, from practically zero in the surface layers to a mean of 65% below 70 m (Table 3). This result was not unexpected. The presence of high proportions of non-cod eggs in the deeper water layers in these areas was known from previous studies using visual identification. However, more interesting, no haddock and modest amounts of coalfish eggs were observed in the Lofoten samples (Table 2), despite the rather common occurrence of ripe specimens from these two species in commercial landings. It may seem that haddock and coalfish do not contribute substantial proportions of eggs to the routine skrei egg collections in area A, and that their suspected effect on the reliability of previous skrei egg surveys thus has been minor. However, our samples in this pilot study were drawn from the center of the skrei spawning area during maximum spawning period and may thus not be representable. A broader sampling program should be undertaken as a basis for firm conclusions on this matter.

The buoyancy distribution of Norway pout eggs is obviously different from that of cod eggs (Table 3). It is expected that their deeper position in the water column will affect the rate at which they are transported northwards by the Nor-

wegian Coastal Current, which sweeps these areas (Fig. 2) and carries skrei eggs and larvae to the nursery grounds in the Barents Sea. This expectation was confirmed by the analyses of planktonic eggs collected in the Coastal Current in area B. In these waters the species distribution of pelagic eggs was quite different from that in the spawning area proper, although cod was still the predominant species in these egg samples. About 570 eggs were analyzed, but only one egg from Norway pout, which had contributed significantly to the egg mass in area A, was detected (Table 2). This lack of eggs from Norway pout in area B possibly reflects the deep position of these eggs in area A; as a consequence they are less likely than cod eggs to be transported by the Coastal Current. Eggs from coalfish and plaice were also present in area B, and one single egg with a rare pattern, identical with that of adult dab muscle tissue (Table 2, Fig. 5C, and Fig. 7).

Samples from the distinct concentration of early development stage eggs with the pronounced westward distribution in area B (cf. introduction) were collected in 1982. The samples contained very high proportions of haddock eggs; from 17 to 100% in individual samples. In fact, they contributed most of the haddock eggs observed in area B in 1982. This valuable information will serve as a basis for further investigations.

These results exemplify the potential of the described biochemical genetics techniques to deal with difficult identifications by means of minute protein samples. Representing an extension of the available tools, the methods may be useful for other applications, in research.

Acknowledgments

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NOTES

Cooling Water Flow Velocity in Relation to Collection of Entrained Larval Fish at Power Plants

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LESLIE, J. K. 1983. Cooling water flow velocity in relation to collection of entrained larval fish at power plants. Can. J. Fish. Aquat. Sci. 40: 370–373.

Velocity of condenser cooling water at numerous sampling sites at some Great Lakes power plants was examined in relation to larval fish entrainment. Current velocity was found to differ significantly in many cases at all depths, for sampling locations spaced 1 m apart in the vertical plane. Extensive use of current meters showed that a simple, presampling study of current velocity at the intake or discharge could improve the accuracy of entrainment estimates.

Key words: current velocity, larval fish, entrainment sampling, power plant

LESLIE, J. K. 1983. Cooling water flow velocity in relation to collection of entrained larval fish at power plants. Can. J. Fish. Aquat. Sci. 40: 370–373.

Nous avons mesuré la vitesse du courant d'eau de refroidissement des condenseurs à de nombreux sites d'échantillonnage à quelques centrales électriques des Grands Lacs en relation avec l'entrainement des larves de poissons. On a constaté que la vitesse du courant diffère de façon significative d'une profondeur à l'autre, dans de nombreux cas, à des sites d'échantillonnage espacés de 1 m verticalement. Plusieurs mesures à l'aide de courantomètres démontrent qu'une étude, avant l'échantillonnage, de la vitesse du courant à l'entrée ou à la sortie de l'eau améliorerait la précision des estimations d'entrainement des larves.

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SAMPLING for larval fish in the condenser cooling water at a power plant should be the least difficult aspect of an entrainment study, as larvae are delivered, without human involvement, from local waters for sampling considerations. The investigator is faced with problems concerning the type of samplers, and the intensity, duration, and frequency of their use. One aspect of entrainment sampling that is seldom given deserved attention, and which is critical to nonselective sampling, is the placement of larval fish nets in relation to current velocity. A simple presampling study of water velocity can help an investigator decide on the appropriate number of samplers and their optimum placement. This study was conducted in 1980 to examine the extent of differences in cooling water velocity through a vertical plane in relation to collection of larval fish at three Great Lakes power plants.

Materials and methods — Condenser cooling water at three Great Lakes power plants, Lakeview Generating Station (GS), Lambton GS, and Nanticoke GS, was sampled with current meters. Lakeview GS sampling took place from a bridge at the discharge whereas Lambton GS and Nanticoke GS were sampled from intake structures. Larval fish nets were used at all stations, but larvae were sufficiently abundant only at Lambton GS.

Lakeview GS is a coal-fired power plant located near Toronto, and has a generation capacity of 2.4 MW. Cooling water from Lake Ontario is drawn via a 730-m-long intake canal to the pumphouses, whereas the discharge is a 152-m-long, 24-m-wide canal. Lambton GS is located on the St. Clair River (Leslie et al. 1979), and Nanticoke GS on Lake Erie (Wiancko 1981).

The velocity distribution of influent or discharged cooling water was determined with five calibrated General Oceanic model 2030 current meters, and one Rigosha flowmeter, each mounted centrally in stabilized, weighted, steel rings. These meters indicated mean current velocity during the 10-min sampling time. Paired, remote-reading current meters (Leslie and Leslie 1980) were used to examine, in cursory fashion, temporal water velocity at numerous locations near the surface.

At Lakeview GS, six current meters simultaneously mapped current velocity at 23 horizontal positions at each of three depths. A maximum of five current meters, spaced horizontally 2 m apart, were similarly suspended along the

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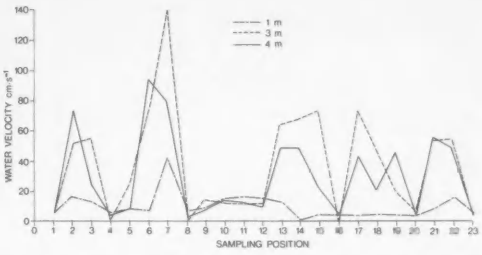

FIG. 1. Current velocity measurements at 23 horizontal points and three depth strata (1, 3, 4 m) at the discharge gates at Lakeview Generating Station, Lake Ontario.

face of intake bar racks at Lambton GS. Eleven fixed sampling positions above the 5-m-deep, 'T'-shaped forebay were used. Two sampling sites were chosen at Nanticoke GS. At one locale, meters were hung from a platform in front of an intake pumphouse and the three-point measurement technique used (Troskolanski 1960). At the other site, meters were set at the 5-m stratum from a bridge over the forebay of the western intake conduit (Foster and Wheaton 1981). Paired remote-reading meters were also used at 0.5 and 1.0 m for short-term (1 min) measurements.

The three-point method of velocity measurements in streams was used at all power plants. In this method, observations are taken of the horizontal water velocity at 0.2, 0.6, and 0.8 maximum depth at numerous points evenly distributed throughout the water column. The average velocity of the 0.2- and 0.8-depth observations is averaged with that of the 0.6 depth to provide a mean velocity at each sampling position. In effect, the sampling areas at each power plant were divided into horizontal and vertical planes. At each point of intersection of these planes, local flow velocity was measured.

At Lambton GS, up to six larval fish nets (0.5 m-diameter, 0.363-mm mesh) were set simultaneously for 10 min to determine if differences in the catch and current velocity across a section of the water column were related. There were two replicates at each of six horizontal points at the 0.2-depth stratum, whereas directly below, at 0.6 and 0.8 depth, single samples were taken.

The concentration of larval fish at each of 14 grid points was expressed as the number of fish caught per 100 cubic metres of water sampled.

Results — Lakeview GS — Current velocities across the entire face of discharge gates (Fig. 1) showed velocity minima at sampling points 1, 4, 8, 16, 20, and 23, reflecting the influence on current flow of bridge-support structures. A summary of flow velocity at 69 points (23 horizontal positions, three strata) is given in Table 1. Velocity at each stratum fluctuated notably. Within a distance of 1 m, mean current velocity through the vertical plane ranged from 0 to 1.4 $m \cdot s^{-1}$ in the X-axis, and from 0.8 to 1.4 $m \cdot s^{-1}$ in the Y-axis.

Nanticoke GS — Current velocities near an intake pump house on June 4, 1980, were similar at all locations (Table 2).

TABLE 1. Current velocity measurements at discharge sampling locations at Lakeview Generating Station, Lake Ontario, 1980. $\bar{x}$ = mean, SD = standard deviation, CV = coefficient of variation, n = 23 for all measurements, and 0.2 maximum depth is defined in Materials and Methods.

Depth strata (m)	Velocity ($cm \cdot s^{-1}$)			
	Range	$\bar{x}$	SD	CV (%)
1 (0.2 maximum depth)	0–42[a]	9.4	8.5	90
3 (0.6 maximum depth)				
Measured	0–140[b]	37.3	35.8	96
Calculated	0–101	28.4	25.0	88
4 (0.8 maximum depth)	2–94	29.5	28.1	95

[a]Velocities at maximum depths of 0.2 and 0.6, 0.2 and 0.8 compared; t = 3.8, and 3.7, respectively (significantly different at P = 0.05).

[b]Velocities at maximum depths of 0.6 and 0.8 compared; t = 0.7 (difference not significant at P = 0.05).

Remote-reading current meters verified values (~40 $cm \cdot s^{-1}$) obtained with digital current meters. The average velocity at 0.6 depth was practically the same as the calculated, or expected, value (Table 2), suggesting approximately laminar flow through the vertical plane.

Current velocity at nine positions at a depth of 5 m across the breadth of the western intake canal on June 20, 1980, averaged (n = 20) 54.2 ± 25.8 $cm \cdot s^{-1}$. Current was ~10 $cm \cdot s^{-1}$ at one side of the intake canal, increased sharply and leveled at ~75 $cm \cdot s^{-1}$ across its breadth, then fell to 10 $cm \cdot s^{-1}$ at the other side of the canal.

Spot checks at 0.5 and 1.0 m with remote-reading current meters revealed alternate bursts, followed by subsidence and reversal of current direction. At the 0.5-m stratum, current velocity was usually higher and spanned a greater range than at the 1.0-m stratum.

Lambton GS — Intake current velocity at Lambton GS on May 21, 1980, was greater and varied less (Fig. 2) than at Lakeview GS and Nanticoke GS. At 11 positions, spaced 2 m apart horizontally, the coefficient of variation (SD $100/\bar{x}$) at the 1-m stratum was 58%, and current velocity was 55.8 ± 32.4 $cm \cdot s^{-1}$. Values at the 3- and 4-m stratum were 41% (54.8 ± 22.4 $cm \cdot s^{-1}$), and 50% (52.0 ± 26.2 $cm \cdot s^{-1}$), respectively.

Larvae were in greatest abundance at sampling position 2 (Table 3 and Fig. 2), which is 3 m from the concrete wall at the distal side of the forebay. Sampling with nets (n = 20) on May 21, 1980, resulted in a catch of 333 yolk sac rainbow smelt, *Osmerus mordax*, and two other species. The concentration of larvae throughout the sampled grid differed considerably.

A combined graph of three-point current measurements at the three power plants (Fig. 3) shows the magnitude of error that would result in determining the flow through a given section if a velocity "index" point were located at 0.2 depth in that section (Craig 1963). At Lakeview GS, the average velocity of 0.2 plus 0.8 depth showed no obvious relation to that at 0.2 depth. Thus, sampling error may be excessive if 0.2 depth were an "index" depth. On the other hand, 0.2 depth

TABLE 2. Current velocity at an intake site at Nanticoke Generating Station, Lake Erie, 1980. $\bar{x}$ = mean, SD = standard deviation, CV = coefficient of variation, n = number of measurements.

Depth strata (m)	Velocity range ($cm \cdot s^{-1}$)	$\bar{x}$	SD	CV (%)	n
1 (0.2 maximum depth)	18–44	35.6	9.7	27	18
3 (0.6 maximum depth)					
Measured	22–43	36.0	8.2	23	6
Calculated	26–43	37.0	6.8	18	6
5 (0.8 maximum depth)	34–43	39.3	4.2	11	6

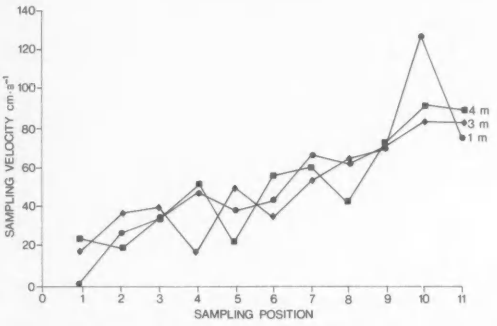

FIG. 2. Current velocity ($cm \cdot s^{-1}$) across intake bar racks at three depth strata (1, 3, 4 m) at Lambton Generating Station, St. Clair River, Ont.

TABLE 3. Concentration of larval fish (larvae · 100 m^{-3}) based on catch at each of 14 grid points across intake bar racks, Lambton Generating Station, St. Clair River, Ont., on May 22, 1980. Value[a] in parentheses refers to current velocity in $cm \cdot s^{-1}$. ns = not sampled with nets.

Depth strata (m)	Sampling position					
	2	4	6	8	10	11
1[b]	44	1	0	118	1	18
	(27)	(50)	(45)	(62)	(127)	(81)
3	22	5	20	0	ns	ns
	(38)	(18)	(38)	(63)	(87)	(87)
4	71	0	33	0	ns	ns
	(20)	(52)	(57)	(42)	(94)	(91)

[a]No significant difference ('t' test; $P = 0.05$) among current velocities at each stratum.
[b]Average of two replicates.

would have served as an "index" depth at Nanticoke GS and Lambton GS.

Discussion — The present study has indicated that the variability in cooling water velocity at power plant intake and discharge locations is probably a factor in abundance estimates of larval fish. Considerable differences in current velocity can exist not only at various locations in the same intake or discharge, but within a shallow vertical sampling

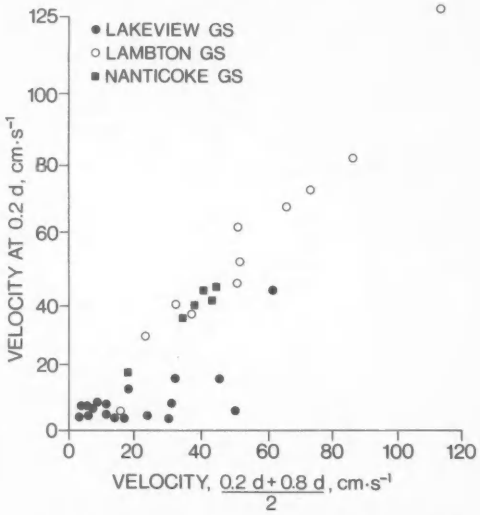

FIG. 3. Combined graph of Lakeview Generating Station, Lambton Generating Station, and Nanticoke Generating Station current velocity determinations for "indexing" at 0.2 maximum depth (d).

grid which extends laterally a few metres. Different current regimes were observed at two adjacent sites in the intake of Nanticoke GS, and at the Lakeview GS discharge, current flow through a vertical plane varied from static to high velocity within a space of 1 m, both horizontally and vertically. Although approximately laminar flow was evident at the Lambton GS intake, there was dissimilarity in the number of entrained larvae at most positions of the sampling grid (Table 3). Differences in current velocity through the vertical plane doubtless affected the catch, as at least four nets were simultaneously set at the same stratum for the same duration and were no more than 2 m apart.

The location of passive samplers relative to the distribution of larvae affects the quantity of fish that are caught. Planktonic, maimed, and dead larvae are likely to be concentrated at the bottom of a channel, where high velocity currents may carry them beneath nets. Similarly, viable young fish may concentrate in quiescent areas of an intake forebay, where samplers are not usually placed. An "index" depth will not be feasible if there are violent alternations in current flow

throughout the water column, as there will be alternate capture and release of some of the larval fish when current flow momentarily peaks, then reverses direction. In this regard, remote-reading current meters are helpful for providing finer details of current velocity at each sampling position, and can quickly locate areas that are unsuitable for passive sampling. It is thus important that a cursory investigation of the current regime at the sampling site be undertaken prior to selection of sampling points.

In conclusion, with a relatively minor increase in sampling effort, methods that are designed to account for the spatial distribution and transport of larval fish in cooling water are likely to increase the accuracy of entrainment estimates. To this end, it is suggested that if passive sampling is planned, mapping of current velocity through various vertical planes should be effected. Subsequently, optimum sites may be sampled, and abundance estimates for the whole water column integrated. Alternately, large active samplers that filter as much of the plant intake volume as is practical should be used in intake or discharge channels, where laminar flow is most likely to exist. Sampling should also involve a number of nets, which may be set in time-stagger, if necessary.

Acknowledgments — W. H. Hyatt, J. E. Moore, and C. A. Timmins assisted with field sampling. Thanks are due to Ontario Hydro for access to power plant sampling areas, and to the CCIW Drafting Section for figures.

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Isolation of Colloidal Fibrils from Lake Water by Physical Separation Techniques

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BURNISON, B. K., AND G. G. LEPPARD. 1983. Isolation of colloidal fibrils from lake water by physical separation techniques. Can. J. Fish. Aquat. Sci. 40: 373–381.

A colloid fraction, highly enriched for organic fibrils, can be isolated routinely by physical means. The physical isolation scheme used here provides gram quantities of undenatured samples in a short time from the epilimnion of a small mesotrophic lake. The total scheme is described in detail and is accompanied by an assessment of yield and contamination at each individual step using a transmission electron microscope as a monitor. The potential importance of organic fibrils is emphasized by a 1980 summer measure showing a fibril fraction to contain three times more carbon than the conventional particulate organic carbon fraction (POC) and 33% of the total dissolved organic carbon (DOC).

Key words: colloids, hollow-fiber ultrafiltration, dissolved organic carbon

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On peut isoler de façon routinière, par moyens physiques, une fraction colloïdale riche en fibrilles organiques. La méthode utilisée fournit rapidement des échantillons non dénaturés prélevés dans l'épilimnion d'un petit lac mésotrophe. Le présent article contient une description détaillée de tout le schéma et une évaluation du rendement et de la contamination à chaque étape, un microscope électronique à transmission servant de moniteur. Un relevé effectué à l'été 1980 fait ressortir l'importance potentielle des fibrilles organiques. On constate en effet qu'une fraction de fibrilles contient trois fois plus de carbone que la fraction de carbone organique particulaire conventionnelle (POC) et 33 % du carbone organique dissous (DOC).

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THE role of nonliving organic materials in lake metabolism is receiving increasing attention (Paerl et al. 1975; Wetzel 1975; Leppard et al. 1977; Burnison 1978), with some of it being focused on organic colloids (Leppard et al. 1977). One class of organic colloid (as defined by electron microscopy in terms of form, dimensions, and capacity to bind heavy metal stains) is now known to be widely distributed and frequently abundant (Massalski and Leppard 1979a, b). This class of colloid is called a "fibril," meaning small string, of which there are several morphological varieties found in lake waters. Fibrils are distinguished from true particles according to the colloid definition established by Vold and Vold (1964), and they are implicated in important lacustrine events such as ion binding by biota (Leppard et al. 1977), flocculation of small particles (Massalski and Leppard 1979a), and microbial community formation (Massalski and Leppard 1979b). They are being increasingly implicated in adhesion phenomena and bacterial microcolony formation in streams (Geesey et al. 1977, 1978). The roles of these fibrils in the freshwater environment may be indeed similar to those of polysaccharides found in soil (metal binding, Martin 1971), sediment (food for benthic animals, Hobbie and Lee 1980), and estuarine environments (sorption of herbicides, Means and Wijayaratne 1982). Precise quantitative information on fibril function in lake water does not exist; consequently, postulated roles have been based on a combination of qualitative observation and a harmonious fit with accepted limnological thinking.

Our long-term objective is to assess some probable natural roles of fibrils with the intent of understanding their significance in modifying known lake processes. To begin, it is necessary to assay fibrils for the nature and extent of relevant physicochemical and physiological activities under controlled laboratory conditions. To this end we report here the procedure we developed to isolate fibrils from lake water by physical means to provide undenatured samples.

Methods — Offshore epilimnetic water from St. George Lake, a small intensively studied lake in a region of Pleistocene kame moraines near Toronto, Ont., Canada (43°57′30″N; 79°25′30″W), was sampled on July 9, 1980. One hundred litres of water were filtered immediately in the field through a nylon Nitex 30-μm screen into 20-L Nalgene containers. The sample was transported immediately to the National Water Research Institute in Burlington, Ont., for further processing. The high molecular weight (HMW) materials were isolated by a modification of a procedure to isolate HMW polysaccharides (Burnison 1978). Figure 1 illustrates the procedure followed. The above modification was the use of a hollow-fiber filtration unit (BST-1, Nuclepore, Pleasanton, CA) instead of a membrane ultrafilter. The hollow-fiber unit had a molecular weight cutoff of 50 000 daltons and a filtration area of 0.5 m^2. The procedure is designed to provide rapidly a high yield of fibril-rich colloidal materials from lake water. Standard water quality data for St. George Lake on July 9, 1980, are listed in Table 1 (D. R. S. Lean unpublished data).

The isolation procedure was monitored by transmission electron microscopy (TEM). The >30-μm fraction was removed from the upper surface of the Nitex screen and centrifuged at 1400 *g* for 10 min. All subsequent filtrations were done with positive pressure (helium at 68.9 kPa). The <30-μm fraction retained on the prefilter (Nuclepore P040, which had been precombusted for 2 h, 450°C) and on the membrane filter (Sartorius SM 11106) were monitored immediately after filtration. The filtrate was stored at 5°C until it could be processed through the hollow-fiber unit. The material retained on the hollow-fiber membrane ("colloid" fraction) was back-flushed with distilled water and filtered through a 0.45-μm membrane filter again to remove bacteria which passed the previous filtration steps. Both the "colloid" fraction and the "soluble" fraction were subjected to ultracentrifugation (105 000 g for 2 h at 5°C in an IEC B60 ultracentrifuge). Pelleted materials were monitored by TEM. A blank control was run through the entire procedure, using distilled water, and again each step was monitored by TEM.

The initial TEM fixative consisted of 2.6% glutaraldehyde and 0.05% ruthenium red (Polysciences Inc., Warrington, PA) in 0.067 mol/L cacodylate-HCl buffer, pH 7.0 (Hayat 1970), applied at ambient (22°C) temperature for 2 h. Two washes of 20 min each were done in buffered, dilute (0.03% then 0.015%), ruthenium red starting at ambient and finishing at 4°C. The second fixative, consisting of 1.33% osmium tetroxide and 0.05% ruthenium red, in above buffer, was then applied, on ice, for 2 h. Mixing of the osmium tetroxide and ruthenium red was done immediately before use. A series of 20-min washes on ice was carried out beginning with buffered, dilute, ruthenium red and then proceeding through dilute buffer to a solution of 20% acetone in distilled water. After dehydration by solvent exchange using a graded acetone series, all samples were embedded in Spurr's (1969) hard epoxy medium. According to the general approach to microtomy outlined in Leppard et al. (1977), silver sections were cut with a diamond knife, mounted on copper grids without support, and stained with uranyl acetate (2% in 50% methanol) followed by Reynold's (1963) lead citrate. Observations and photographs were made with a Philips 300 electron microscope. Light microscopy was used to ascertain pellet

TABLE 1. Physicochemical water quality data for St. George Lake (0–1 m) taken on the week of July 9, 1980.[a]

Temperature	21.5°C
pH	8.1
Dissolved organic carbon	8.7 mg/L
Dissolved inorganic carbon	33.0 mg/L
Oxygen	8.8 mg/L
Particulate organic carbon	0.88 mg/L
Particulate organic nitrogen	0.11 mg/L
Total phosphorus	0.03 mg/L
Total K–nitrogen	0.67 mg/L
$N-NO_3$	0.04 mg/L
$N-NO_2$	0.01 mg/L
$N-NH_3$	0.00 mg/L
Ca	44.0 mg/L
Mg	7.3 mg/L
Fe	0.1 mg/L
Mn	0.03 mg/L
Conductivity	335 μmhos·cm^{-1}

[a]Much of the organic debris was derived from a decaying *Volvox* population.

TABLE 2. Morphological observations on the physical separation scheme.

Fraction	Resolution level	Description
Large particles >30 μm	Visible light	Zooplankton, parts of zooplankton, debris, microbes, colonies of microbes, granules, bits of algal cell wall, helical structures, small algae
	TEM	Many cell and organism types, many kinds of debris, many tripartite structures resembling membranes, some bacteria–plant debris associations, many diverse colloids trapped in depressions of the surface of large irregular debris particles
		Fibrils almost negligible as a portion of retained material which in turn is a small portion of total organic carbon
Small particles (upper surface of prefilter)	Visible light	Many rounded microbial cells including *Anabaena*, some long cylindrical cells and small encapsulated cells, some *Scenedesmus* cells
	TEM (Fig. 3)	Large prokaryotes, small prokaryotes including filamentous forms, diatoms, and frustule parts, apparent membranes and bits of exoskeleton, some large cysts and amoeboid-like organisms
		Fibril masses per se not present Some fibrils associated with some particles Some scattered individual fibrils near surface
Small particles (within the prefilter)	Visible light	Some small particles difficult to identify
	TEM (Fig. 4)	Small parts of cells and small bits of exoskeleton, some apparent membranes, rarely a small prokaryote
		Fibril masses per se not present
POC–DOC cutoff: membrane filter (upper surface of filter)	Visible light	Sparse, patchy distribution of particles near resolution limit
	TEM (Fig. 5)	Large colloids almost entirely absent
		Fibrils rare to absent
POC–DOC cutoff: membrane filter (within the filter)	Visible light	Sparse, patchy distribution of particles near resolution limit
	TEM (Fig. 6)	More than 99% of pore space empty with rare views of bacteria of extremely small diameter
		Fibrils absent
Colloids (and biota in upper range of colloidal dimensions)	Visible light	Irregular sheets plus very small granules
	TEM	Bacteria of 0.4-μm diameter and less, apparent membranes, submicroscopic vesicles, small granules, some viruses and virus aggregates.
		Fibrils in great abundance Fibrils often present as discrete aggregates Note: When the colloid fraction was first treated with a flocculant and then pelleted, it was shown to contain fibrils greatly in excess of all other colloid types taken together (compare Fig. 7 and 8)
Solubles	Visible light	No material pelleted unless the soluble fraction was first treated with a flocculant — the resultant pellet

TABLE 2. *(Continued)*

Fraction	Resolution level	Description
		contained very small granules aggregated into irregular particles of various sizes up to 100 μm diameter.
	TEM (Fig. 9)	Aggregates of granules, shortened fibril-like structures of irregular diameter, some very small flakes
		Fibrils absent

heterogeneity and the degree of patchy distribution of materials retained at and near filter surfaces.

The "colloid" fraction was also examined by freeze-etching. A sample was dispersed in a drop of distilled water which subsequently was vitrified by rapid freezing in liquid Freon 12 followed by liquid N_2. The handling, fracturing, and freeze-etching were done in the standard way (Moor 1971) on a BA 360 M Balzers apparatus. The replicas were cleaned according to Leppard and Ramamoorthy (1975) and placed on grids without support films for examination by a Philips 300 TEM.

The "colloid" fraction and the 0.45-μm filtrate were analyzed for carbon, as DOC, by the Total Organic Carbon Analyzer (Beckman, model 915). This instrument removes dissolved inorganic carbon by acidification; the remaining DOC is combusted by ultraviolet light to CO_2 which is determined by an infrared analyzer.

Results — Morphological observations on the sequential separation of particle types (both "classically defined particles" and colloids, Table 2) are illustrated by photographs representing general views studied at ~3-nm resolution (shown in the same sequence as for Fig. 1) in Fig. 2A, B, C; Fig. 3, 4, 5, 6; and Fig. 7, 8, 9, 10. Figure 2 (A, B, C)

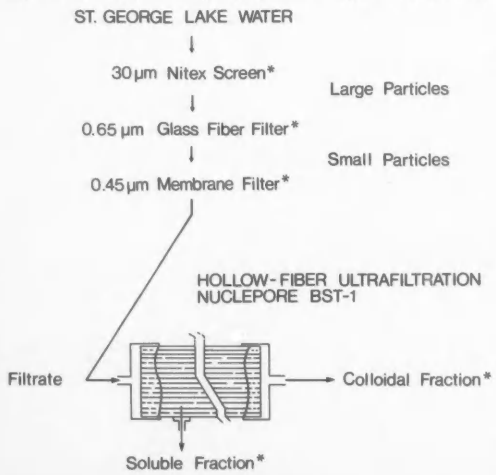
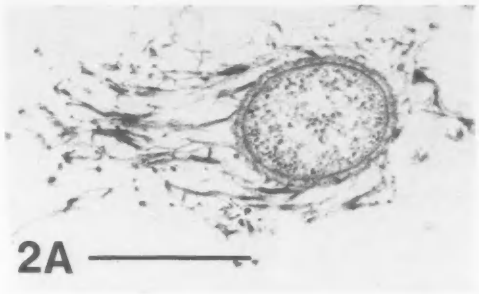


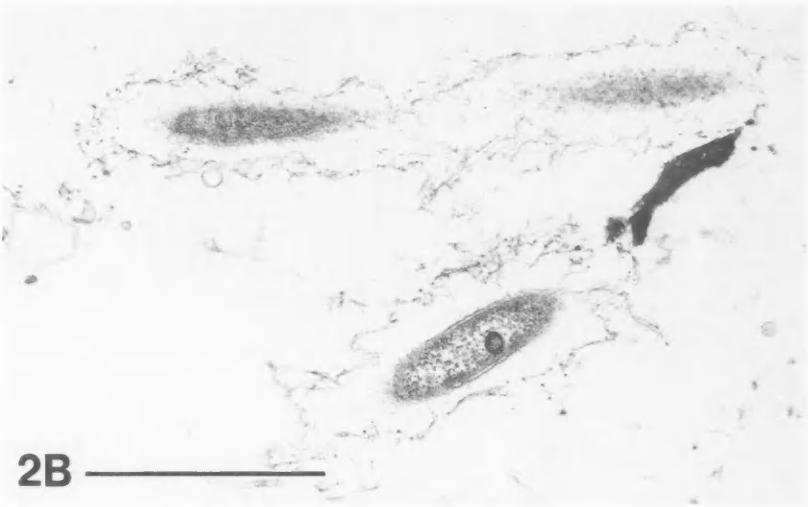
FIG. 1. Isolation of colloidal fibrils from lake water by physical separation. *Observed by transmission electron microscopy.

suggests bacterial and algal origins for some of the fibrils in St. George Lake. Much of the morphological evidence suggests that sheath material from common mucilaginous algae may contribute heavily to the "fibril burden" of the water, a suggestion compatible with observations made earlier by Drews (1973) and by Kessel and Eloff (1975).

Some senescent phytoplankton cells were observed in the large-particle (>30 μm) and small-particle (<30 μm) fractions when viewed by TEM. However, senescent cells were also seen in phytoplankton from water samples which did not undergo filtration. We have kept the positive filtration pressure to less than 70 kPa to avoid possible filtration damage. On the Nitex screen, many large particles having an irregular surface acted as traps for colloids, but trapping of fibrils appeared negligible. Although the 0.45-μm filter was used as the arbitrarily defined cutoff separating "classical particles" from soluble and colloidal material, the principal separation of this nature really occurred at the upper surface of the prefilter. There was a sharply defined exclusion of small particles at this surface relative to what lodged within the prefilter pore structure and to what was retained at the upper surface of the membrane filter. Because the 0.45-μm filter also passed bacteria of very small dimensions, in addition to sedimentable fibrils, it clearly did not yield a filtrate which could properly be considered to contain DOC exclusively. Ultrafiltration concentrates these particles as well as the HMW materials in the "colloid" fraction. Ultracentrifugation was used to separate these particles from the soluble HMW components. The "colloid" concentrate therefore contained these non-soluble components, which were subsequently removed by ultracentrifugation. The pellet obtained was a heterogeneous mixture of ribbon-like fibrils and other colloids (Fig. 7). The addition of a flocculating agent (ruthenium red, final concentration 0.007%, Luft 1971) to the ultracentrifuge supernatant precipitated a very fibril-rich material (Fig. 8). Chemical analysis of the supernatant for carbon (as DOC) gave a value equivalent to 2.88 mg C/L. The total DOC for July 9, 1980, was 8.7 mg C/L and the particulate organic carbon (POC-dry combustion) was 0.88 mg C/L (Table 1). Therefore, the isolated colloidal fraction is 33% of the TDOC and over three times the POC content.

The "soluble" fraction (<50 000 mol wt) produced an insignificant pellet by ultracentrifugation, but a precipitate was formed upon addition of ruthenium red (Fig. 9). The concentration of these small fibrillar-granular units, which may be lower molecular weight components of the fibrils, was considered to be negligible, and this fraction was not studied further.





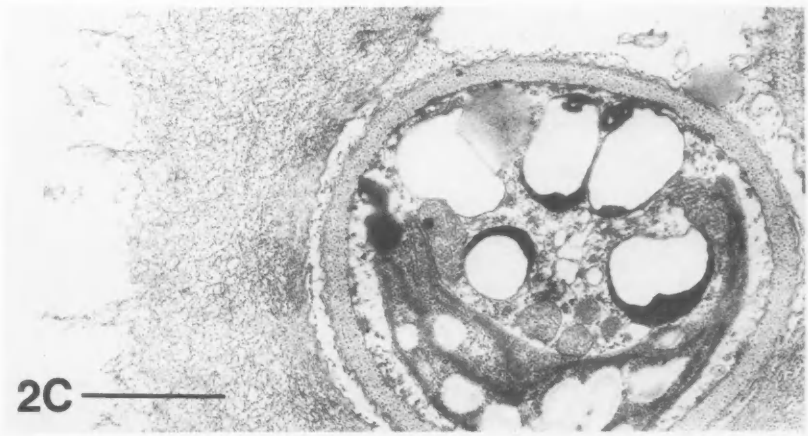


FIG. 2. Fibril–biota associations which pass the 30-μm screen. Those associations retained by the screen tended to be too complex, as seen in sections, for ready interpretation of a single micrograph. Interpretations based on series of sections are found in Table 2. Figure 2A shows a bacterial cell bearing fibrils, possibly in the act of shedding some of them. Bar represents 0.5 μm. Figure 2B shows a loose association of bacteria, each of which bears a capsule of fibrils. Bar represents 1 μm. Figure 2C shows a eukaryotic algal cell enclosed within a dense layer of fibrils. Bar represents 1 μm.

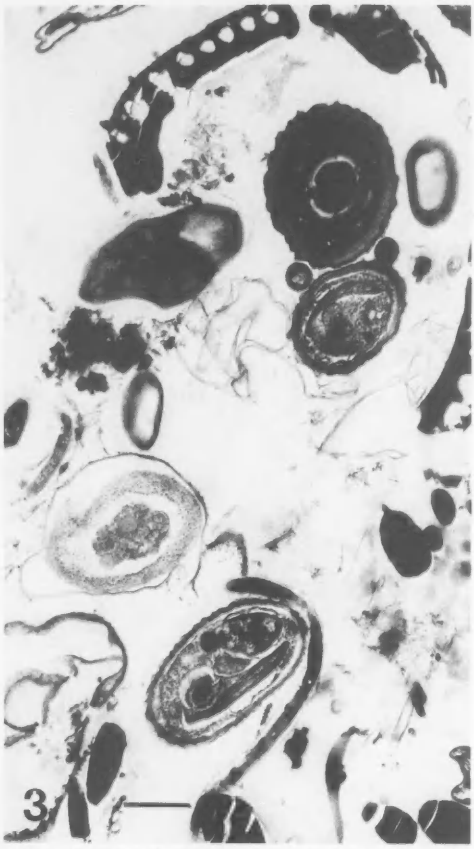


FIG. 3. Glancing section through the upper surface of the prefilter showing particles, including cells, retained by the upper surface. Bar represents 1 μm.

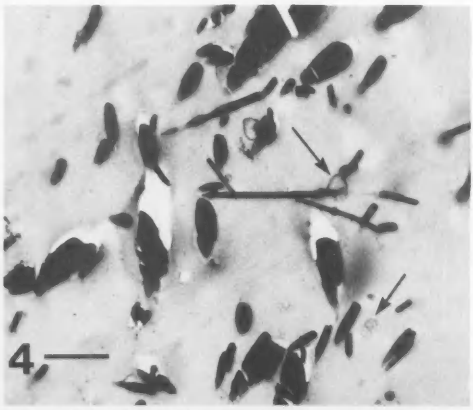


FIG. 4. Section through the midlevel of the prefilter showing its substructure and a near absence of recognizable (see arrows) biological structures. Bar represents 1 μm.

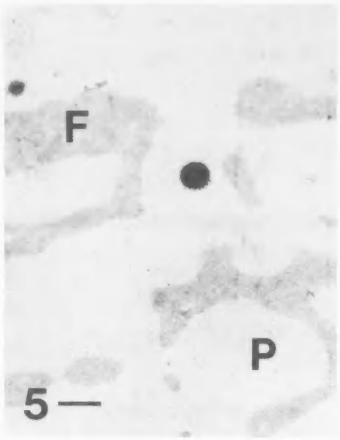


FIG. 5. Glancing section through the upper surface of the 0.45-μm membrane filter. Note that the only "particle" present in the pore space is a bacterium which is obviously smaller than the pore lumen. In this and in the subsequent figure, the filter material is labeled "F" and the pore space "P." Bar represents 1 μm.

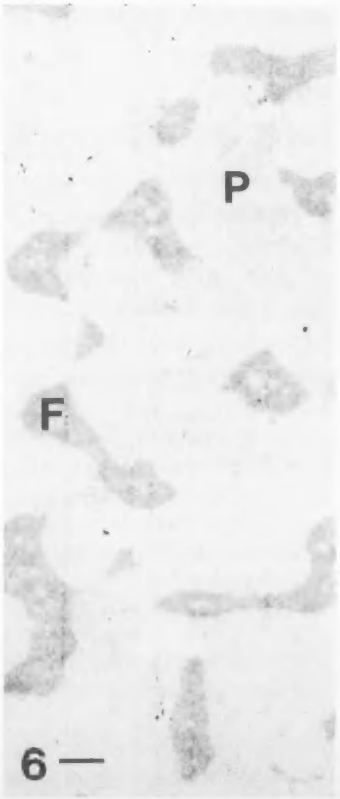


FIG. 6. Section through the midlevel of the 0.45-μm membrane filter. Note the absence of particles in the pore spaces. Bar represents 1 μm.

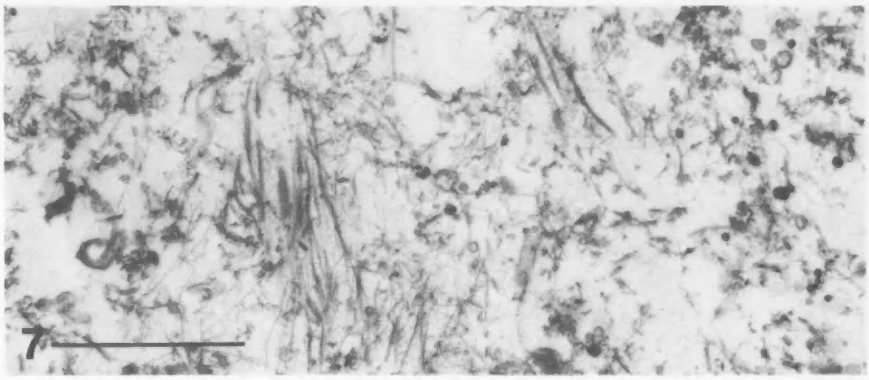


FIG. 7. Sedimentable portion of colloid fraction (105 000 *g* for 2 h at 5°C) revealing ribbon-like fibrils and other colloids. Note that most of the individual particles have at least two dimensions in the lower portion of the colloidal size range. Bar represents 1 μm.

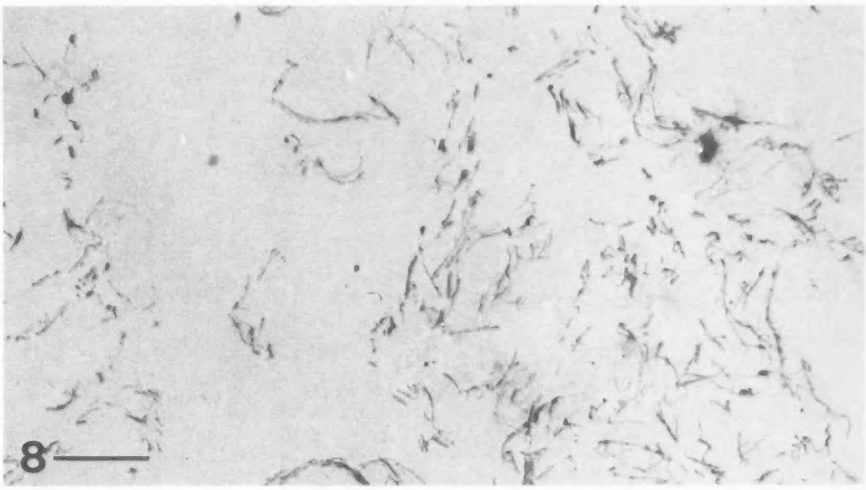
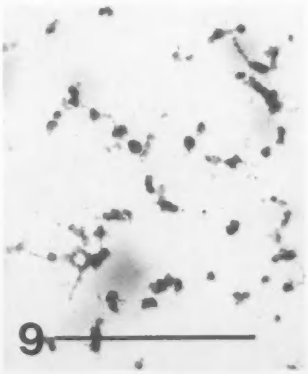


FIG. 8. Nonsedimentable portion of colloid fraction revealing ribbon-like fibrils to be an extremely dominant component. See Results for details on microscopical visualization of this supernatant fraction. Bar represents 1 μm.



The distilled water blank control did not yield any fibrillar structures at any step within the isolation procedure.

Freeze-etching of the "colloid" fraction, in the absence of any chemical treatment of the organics, revealed the fraction to be rich in fibrils (Fig. 10). The appearance of fibrils in a freeze-etch replica is not identical with that of fibrils in a similarly derived fraction which had been chemically stabilized, embedded, and sectioned. Such a morphological difference was noted previously by Leppard and Ramamoorthy (1975). For reasons of geometry some differences may derive from the fact that freeze-etched fibrils are hydrated whereas sectioned fibrils are not (Leppard and Colvin 1978).

FIG. 9. Flocculated "solubles" (<50 000 mol wt) which had been separated from the colloid fraction by ultrafiltration. Bar represents 1 μm.

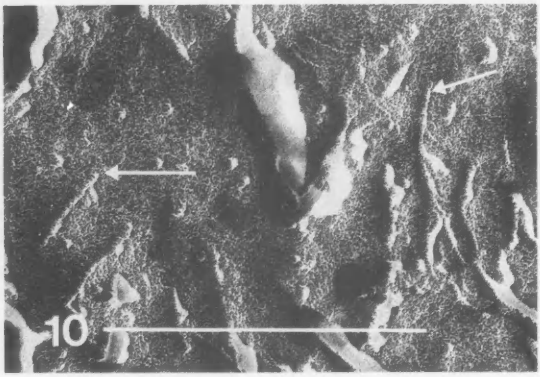


FIG. 10. Freeze-etch view of colloid fraction revealing individual fibrils (see arrows). Bar represents 0.5 μm.

Discussion — A fibril-rich colloid fraction has been isolated from lake water with minimal losses in yield in a relatively short time. This fraction contains a significant amount of organic carbon. Other lakes may not yield the same concentration, as the concentration of the fibrils seems to be dependent on phytoplankton production (Burnison unpublished data). Also, if the water quality were such as to make the fibrils either more rigid or "stickier" with respect to filter surfaces, then fibril yield would be adversely affected. Because the five lacustrine fibril preparations analyzed thus far contain acid polysaccharide (Burnison 1978), their rigidity and adhesion properties could conceivably depend on the ionic composition (Jirgensons 1962; Shuster and Wang 1977) of the specific lake water samples from which they were isolated.

Fibrils often resemble the ultrastructural units of the mucilaginous sheaths of phytoplankton (Fig. 2C) as well as those of bacterial capsules (Fig. 2A, B). Losses in fibril yield at filter surfaces tended to be losses of those fibrils which were structurally integrated with cells as cell surface components. One questions whether such fibrils can be stripped from their cell surface sites as a result of the filtration pressure. The extent of such artifactual production of small fibril aggregates is unknown and the presence of some senescent cells (as expected in nature) complicated analyses for evidence of damage by shear forces. The possibility that the natural loss of fibrils from cell surfaces might be accelerated during filtration leads to the question of the ratio of small fibril aggregates to large ones in the original sample. There is no way yet to determine this, and the situation is complicated because fibrils readily form aggregates with each other and with other kinds of particles.

We have noted that the conventional 0.45-μm membrane filter does not serve as a proper cutoff filter for distinguishing DOC from POC, as previously noted by Breger (1970) and by Sharp (1973). In addition, it does not even serve to keep biota separate from the operationally defined DOC fraction. The major purpose of this membrane filter in our separation scheme is to serve as a reference to relate our fractions to past limnological papers. We realize that ultrafiltration is a very impractical procedure to use routinely for DOC analyses. However, this paper illustrates the complexity of the DOC fraction and that the DOC fraction should not be viewed as a solution of various organic compounds.

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Comments on Estimating Partial Recruitment in Virtual Population Analysis

In a recent note Roff (1981) correctly pointed out that the estimator

$$\hat{R}_t(a) = f'_t(a)/f_t(a)\,\hat{R}^*$$

is not algebraically equivalent to the partial recruitment multiplier for the fishing mortality F_t. He argues that "there is no need to settle for a quick inexact solution as the power of the computer can be brought to bear on the matter" and claims that approximations and numerical methods "would not be necessary if a method of estimating partial recruitment exactly was available. In the next section I present such a method." Equation 14

$$R_t(a) = \frac{-1}{F_t}\log_e\left(p_t(a)\exp[-F_t] + 1 - p_t(a)\right)$$

is presented as that exact solution. The following analysis shows that equation 14 is not an exact solution for the partial recruitment multiplier in catch equation 2. Taking equation 2

$$C_t(a) = \frac{N_t f_t(a)\,F_t R_t(a)\,(1 - \exp[-(F_t R_t(a) + M)])}{F_t R_t(a) + M}$$

and equation 9

$$C_t(a) = \frac{N_t f_t(a)\,p_t(a)\,F_t(1 - \exp[-(F_t + M)])}{F_t + M}$$

and solving for $p_t(a)$ gives

$$\text{(A)}\quad p_t(a) = \frac{(F_t R_t(a) + M R_t(a))\,1 - \exp[-(F_t R_t(a) + M)]}{(F_t R_t(a) + M)\,1 - \exp[-(F_t + M)]}.$$

Catch equation 2 is derived from

$$\text{(B)}\quad N_{t+1} = N_t(a)\exp[-(F_t R_t(a) + M)],$$

and catch equation 9 is obtained from

$$\text{(C)}\quad N_{t+1}(a) = N_t(a)\,(p_t(a)\exp[-(F_t + M)] + (1 - p_t(a))\exp[-M])$$

(Journal's file).

Using B and C Roff obtained relationship 13

$$\exp[-(F_t R_t(a) + M)] = p_t(a)\exp[-(F_t + M)] + \exp[-M](1 - p_t(a))$$

which is the basis for equation 14. Solving equation 13 for $p_t(a)$ gives

$$\text{(D)}\quad p_t(a) = \frac{1 - \exp[-F_t R_t(a)]}{1 - \exp[-F_t]}.$$

When there is no natural mortality ($M = 0$) and in the trivial case where all fish are recruited ($R_t(a) = 1$), A and D agree, but in general the two equations are not equivalent. The reason for this is that equations B and C define different processes. In particular, for a given N_t, N_{t+1} will be the same for both B and C but the trajectories will not coincide (Fig. 1) and consequently the catches will not, in general, be equal. The result is that equation 14 is not an exact solution for the partial recruitment multiplier of the fishing mortality referred to in catch equation 2, as Roff claims, although it could be used as an approximation when natural mortality is small.

An exact solution for use with Baranov's catch equation, the basis for equation 2 (which is not necessarily a more accurate depiction of reality than catch equation 9), can be arrived at by defining $R_t(a)$ as the partial recruitment multiplier for the exploitation rate u_t instead of the fishing mortality F_t. Using this definition:

$$C_t(a) = N_t f_t(a)\,R_t(a)\,u_t$$

where $u_t = F_t(1 - \exp[-(F_t + M)])/(F_t + M)$.
Given that

$$f'_t(a) = C_t(a)/C_t$$

we have

$$\begin{aligned}\hat{R}_t(a) &= f'_t(a)/f_t(a)\,\hat{R}^*_t \\ &= N_t f_t(a)\,R_t(a)\,u_t/C_t\,f_t(a)\,\hat{R}^*_t.\end{aligned}$$

Substituting

$$\hat{R}^*_t = N_t u_t/C_t$$

we get

$$\begin{aligned}\hat{R}_t(a) &= N_t f_t(a)\,R_t(a)\,u_t C_t/C_t\,f_t(a)\,N_t\,u_t \\ &= R_t(a).\end{aligned}$$

Therefore we can write

$$N_t(a) = C_t(F_t + M)/R_t(a)\,F_t(1 - \exp[-(F_t + M)]).$$

Although this expression is computationally equivalent to equation 15 in Roff (1981), its derivation is based on, and it applies to, Baranov's catch equation. In computing $R_t(a)$ the formula:

$$\hat{R}_t(a) = C'_t(a)/C_t(a)\,\hat{R}^*_t$$

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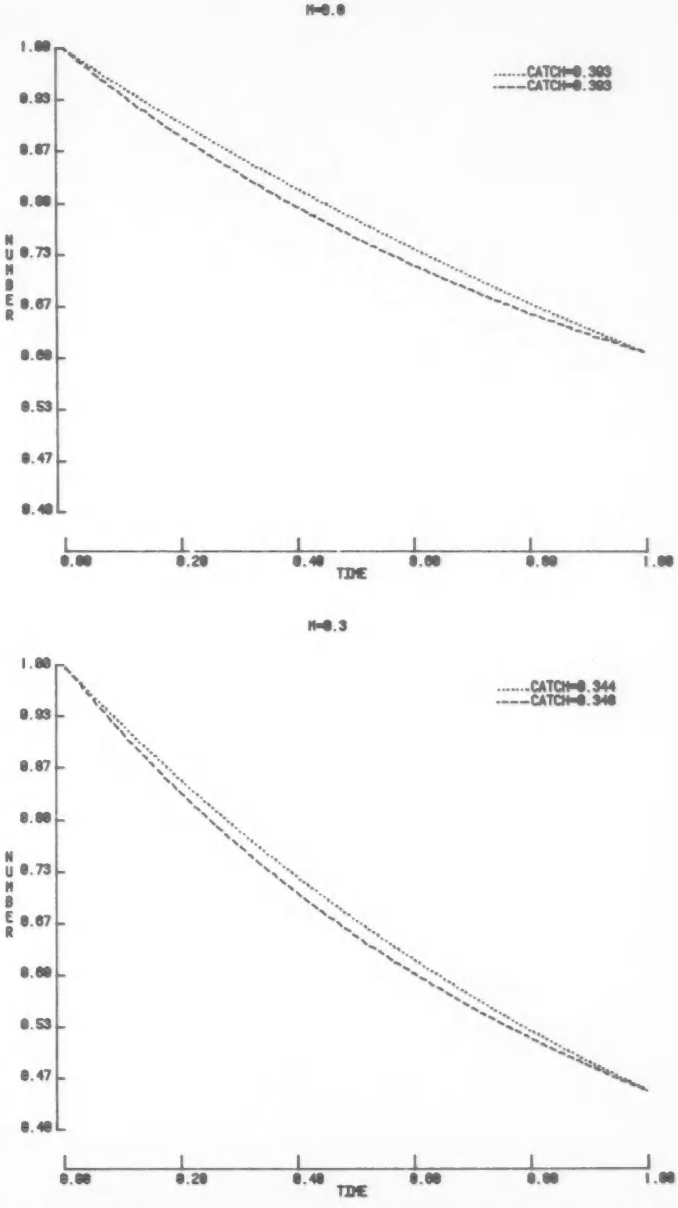

FIG. 1. The time trajectories defined by equation B (···) and equation C (---) will generally differ. For these examples $N_i(a) = 1$, $F_i = 1$, $R_i(a) = 0.5$, and $p_i(a)$ was calculated using equation D. The natural mortality M is indicated and the catches were computed from catch equations 2 and 9.

can be used to reduce rounding error which may be introduced by the extra division. — STRATIS GAVARIS, *Research and Resource Services, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld. A1C 5X1.*

ROFF, D. A. 1981. On estimating partial recruitment in virtual population analysis. Can. J. Fish. Aquat. Sci. 38: 1003–1005.

REPLY

The development of the catch equation proceeds from the premise that fishing mortality is continuous and equal throughout the year. From this we obtain immediately the cohort equation

$$(1) \quad N_{t+1} = N_t \, e^{-(FR+M)}$$

where, for notational convenience, I have omitted the subscripts referring to the particular age a. In the partitioning method we assume that the population is divided "into two portions, a portion that has entered the catchable population and a portion that is still unrecruited" (Roff 1981). From this we get

$$(2) \quad N_{t+1} = N_t \, e^{-(F+M)} \, p + N_t \, (1 - p) e^{-M}$$

where the fishing mortality F is the same in both equations. Assuming that the cohort sizes in equations (1) and (2) must be the same, we obtain the relationship between P and R (equation 14 of Roff 1981). From equations (1) and (2) we can derive via calculus the appropriate catch equations. However, as pointed out by Gavaris (1983), these will not be exactly equivalent. The reason is that in one case we apply a small fishing mortality rate to the whole cohort over the year whereas in the other case we apply a larger rate to a fraction of the cohort. Thus, strictly speaking, the initial population size should be estimated using equation 15 of Roff (1981). However, if the difference between using 15 or the more usual formula is in any degree significant, one would have to question the very use of cohort analysis as both assumptions on the distribution of fishing mortality are equally tenable. The truth, in fact, probably lies somewhere between vulnerability being unequally distributed through the cohort but not in a simple dichotomous fashion. — D. ROFF, *Department of Biology, Stewart Biology Building, 1205, Ave. Dr. Penfield, McGill University, Montreal, Que. H3A 1B1.*

GAVARIS, S. 1983. Comments on estimating partial recruitment in virtual population analyses. Can. J. Fish. Aquat. Sci. 40: 000–000.

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Descriptive Physical Oceanography — An introduction. 4th Edition. *George L. Pickard and William J. Emery. Pergamon Press, New York. 1982. 249 p. $35 (U.S.) hard cover or $11.95 in paper back.*

It gave me very great pleasure to be asked to review the fourth edition of this book, and I was not disappointed. The first edition was received with general praise in the oceanographic community; the second and third editions were substantially the same as the first edition but with cosmetic changes; the fourth, however, marks a significant departure.

The first change of note is the addition of a coauthor, Emery, below Prof Pickard's name. Dr Emery has clearly had a significant impact on the volume. Readers of a recent paper by Emery and Dewar in *Progress in Oceanography* will recognize many of the diagrams added to the fourth edition.

The next change of note regards the table of contents and general organization of the book. The authors have broken the text down under a very large number of headings and subheadings giving a compact structure to each section; this allows the table of contents to be enlarged from 1 to 4 pages with a vast increase in its utility. The type style has been changed to a cleaner, more modern face which makes the book more pleasant to work with. A concomitant change is an increase in the number of words per line and lines per page. I approve of these changes and had in fact complained in the past that I found the narrowness of the typed columns in the early editions rather disconcerting.

So much for the packaging, how about the meat? Since the first edition was released, much has changed in physical oceanography. That was the reason, probably, why it was decided that cosmetic changes were no longer adequate. The section on salinity has been changed substantially and brought up to date including a discussion of the practical salinity scale. In other early sections, changes of a minor nature have been made which serve to tighten the text. Material on upwelling has been deleted from chapter 4 and reemerges, with a little dynamics, in chapter 8, Coastal Oceanography.

Chapter 5 on water, salt, and heat budgets of the world has been substantially expanded and now includes an extremely detailed discussion of the conservation of heat energy. It has always surprised me how complex the heat budget of the ocean turns out to be when at first sight one expects a very simple subject. The inclusion of this material was a farsighted decision.

In chapter 6 I offer my first suggestion for changes to be included in the fifth edition. The discussion of different current meter types is changed and, thankfully, the Ekman current meter receives barely any mention. However, the discussion of different types of current meters is not adequately linked with the discussion of different mooring types. It is now well known that current meters using Savonius rotors (e.g. the Aanderaa RCM4) are incompatible with surface buoyancy on the mooring. This is not a trivial point and it should have been included. The following section on the geostrophic method and dynamic topography is a welcome addition, after all to a large extent the reason for measuring the density of seawater is so that geostrophic computations can be made.

Chapter 7 on the circulation and water masses of the oceans is changed in fairly minor ways. Diagrams have been redrafted and new developments incorporated in the discussion. However, the subject has not changed greatly, with one exception, which leads me to my next recommendation for the fifth edition. Chapter 7 includes a competent discussion of the controversy centering around the C. R. Mann (bifurcating Gulf Stream) and the L. V. Worthington (two-gyre) models of the North Atlantic circulation. Pickard and Emery should have pointed out that the controversy lead Worthington to offer a prize (one case of whiskey) to anyone who could find a circulation scheme for the North Atlantic that conserved water properties *and* was geostrophic everywhere. (Mann's model was geostrophic but nonconservative, and Worthington's the reverse.) The prize was collected by Carl Wunsch, who supplied not one but two models and showed that in fact there were an infinite number of circulation patterns that satisfied Worthington's criteria. A discussion of inverse theory, which Wunsch introduced to physical oceanographers, is beyond the scope of this text, but a discussion of the resolution of the controversy, largely in favor of C. R. Mann's model, is appropriate.

This text book is remarkably free of typographical errors though they are not entirely absent. I was struck by the rather curious adoption of the word "thermostat" as a transitive verb on pages 97 and 98.

At a cost of $11.95 (U.S.) in paper back the book is a bargain. I have owned a copy of the first edition since 1968; however, I intend having a copy of the fourth edition for my personal collection; I recommend that others follow suit.

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(R451)

Salmon Ranching. *Edited by J. E. Thorpe, Academic Press Inc., London. 1980. x + 441 p. $78 (U.S.).*

The acceptance of ocean ranching as an important tool in the management and enhancement of the salmon resource gives this book particular relevance. During almost a hundred years of man's involvement with salmonid populations, procedures have developed from the unsophisticated methods of "egg hatching and fry dumping" into a variety of complex culture techniques involving investigations in the areas of fish health, nutrition, physiology, and genetics.

On a world scale salmon ranching is evolving from an activity devised to compensate for environmental degradation of the natural salmon habitat and to satisfy the needs of sport fishermen into a more aggressive strategy of food production.

It now represents a multimillion dollar industry in several countries of the northern hemisphere and is extending its influence to countries bordering the subAntarctic Ocean. The greater abundance of salmonids available for exploitation together with the increased social and economic benefits for the countries involved has resulted in the development of government policies and legal regulations oriented to the enhancement and protection of this extremely valuable natural resource.

In the context mentioned, the multiauthor volume *Salmon Ranching* is a most timely overview of the current status of salmon ranching in both the northern and southern hemispheres of the globe. To all concerned with salmon, whether interested in the biology of these species, their production and management, or their exploitation and marketing, it provides well-documented information.

The book consists of 20 chapters. An introductory chapter defines the topic and describes the development of salmon culture towards ranching, evaluating the early advances in culture technology and comparing its energy efficiency ratio with other protein-producing systems, the significance of salmon ranching, and the role of international agencies in the regulation of salmon fisheries.

Several authoritative contributors describe in successive chapters 2–11 the history, development, and current status of salmon culture in the USA, Canada, Japan, Western Europe, Iceland, and the Soviet Union. Chapters 12–15 discuss the causes of the failures and successes of the numerous attempted transplants of anadromous salmonid species to Atlantic Canada, the northwestern Soviet Union, South America, and New Zealand. These regional perspectives are succeeded by three chapters which delve in more detail into the development of specific culture technologies. The first of these, chapter 16, by Tom Bilton, describes experiments which are leading to the maximization of ocean survival by the optimization of smolt size and release date in coho salmon. The second of the research and development trio, chapter 17 by Tony Novotny, again deals with manipulation of release timing and size, but here the emphasis is on alteration of migration routes, ocean distribution, and contribution to specific fisheries. The third of these, chapter 18 by Harold Mundie, describes an innovative attempt to optimize the fluvial habitat of coho salmon by constructing a stream with alternating riffle areas for the generation of natural food and sheltered pools for the salmon presmolts. The penultimate chapter by Bill McNeil compares the differing legal aspects of salmon ranching in the Pacific rim countries. In the final chapter John Thorpe reviews the current status of salmon ranching both within and outside of the natural range of individual species and with regard to public versus private involvement. This final chapter also summarizes the viewpoints of a number of writers on the controversial topic of ocean-carrying capacity.

In summary, this volume provides a valuable synopsis of the many topics related to salmon culture for ocean release in most of the countries where it is currently practiced including high seas fisheries, the application of the 200-mile economic zones in sensitive geographical areas, the possible threat of mixed stock fisheries to the natural population of salmon, the risks of modification of the genome in continuously artificially propagated stocks, the effects of manipulation of release location and timing using net pens and a number of others.

One weakness evident in the volume is the lack of coverage of some of the new and innovative salmonid culture techniques such as dietary manipulation of body composition, growth programming, sex control, gene banking, assessment of migration readiness, new incubation procedures, and induced ovulation. However, particularly for its wide-ranging geographic coverage, *Salmon Ranching* should be a valuable addition to every fisheries reference library and to the personal collections of fisheries administrators, scientists, biologists, and culturists.

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Marine Fisheries Ecosystem: its quantitative evaluation and management. *Taivo Laevastu and Herbert A. Larkins. Fishing News Books Ltd., Farnham, Surrey, England. 1981. 162 p., 53 illus. £15.50 + £1.55 post/packing.*

This book will be useful to anyone who is interested in complex simulation models of marine fisheries. In particular, it is background reading for potential users or imitators of the well-known simulation models of the northeast Pacific fisheries, DYNUMES and that ilk, developed by Laevastu and various colleagues.

If this kind of modeling interests you, read the book. There are some editorial lapses and confused or contradictory passages that may give problems to uninitiated readers, but, despite these, the book is a good representative of its genre, and gives a good overview of what is involved in this kind of modeling.

For most fisheries ecologists, however, I suspect that analysis means something more than empirical reductionism stretched to the limit set by the available computing power. Unfortunately, the authors' great breadth and depth of fisheries knowledge is here sufficiently constrained by the limitations of the topic that I couldn't identify much that I thought would interest the general fisheries audience.

Quite clearly, the book deals with a much narrower subject than its title implies. The nub of it is set out by the definition of "holistic simulation" that appears early in the book and is adhered to throughout. "The holistic (structural, deterministic) simulation is defined as: Numerical quantitative reproduction of a system by structural parts of it, using deterministic formulations justified by empirical data." This seems to be saying that holism is nothing more than a whole lot of reductionism lumped together. Certainly this is not a definition I would use nor, I suspect, many others in this post-IBP era. But then again, words are what we choose to make them. This is the definition the authors chose to apply, and they use it consistently.

Their choice of perspective does, however, lead to some statements that appear strange if looked at in a broader context than that of the book itself. For example, the foreword in-

forms us that the model of Anderson and Ursin is "... the only other known fisheries ecosystem (multispecies) model at present ...". Personally, I can think of dozens of models that would qualify, but by my definition of course, not that of Laevastu and Larkins.

To summarize, this is not a book for the general fisheries audience. Unless you are interested in complex simulation models, you can afford to pass it by, although you will miss some interesting empirical details in doing so. If you are interested in this kind of model, then the book is worth reading, although you had better be familiar enough with the subject to interpret your way through the occasional muddled exposition and errors.

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(R436)

The Early Life History of Fish: recent studies. *The Second ICES Symposium, Woods Hole, 2–5 April, 1979. Coedited by R. Lasker and K. Sherman. Rapports et Procès-verbaux des Réunions, Vol. 178. Conseil International pour l'Exploration de la Mer, Palaegade 2–4. DK-1261, Copenhagen K. Denmark. 1981. 607 p. 350 DKr (approx. $40.00 U.S.) plus mailing costs.*

Information about the early life of fishes is increasing dramatically and this volume presents a telescopic view of the variety of studies presently in fashion. An indication of the exponential increase in early life history studies is provided by Smith and Richardson (1979). "The publication rate has risen from approximately one title per year around 1910 to ten per year around 1940 to some fifty per year around 1970." The early life of fishes, as an almost identifiable subunit of the field of Fishery Science, is actively evolving. Readers should be reminded that fishes are unique among all vertebrates; no other vertebrate order has their young occupying so many different habitats and displaying such diverse anatomical features.

The first ICES Symposium was held in Oban, Scotland, in May 1973, under the chairmanship of J. H. S. Blaxter. This, the Second ICES Symposium is divided into six sections. Chairmen were selected and developed introductory overview papers of each discrete subject. It is mainly for this method of organization that the sections are so unequal in length. The contributed papers are divided into Modelling (54 p.), Pollution (53 p.), Enclosure Studies (32 p.), Distribution and Abundance (143 p.), Physiological Ecology (185 p.), Rearing and Aquaculture (56 p.), and Systematics and Development (53 p.). Contributors were mainly marine fisheries people; freshwater studies were far in the minority. A count of authors (duplicates included) resulted in the following continental distribution: North America 151, Europe 87, Asia (Japan and India) 22, South America 4, USSR 3, Africa 3, and the Philippines 1. Thus, this volume consists of, in the main, contributed studies from around the world.

A memorium to Dr Elbert H. Ahlstrom is included, but the editors failed to mention that Dr Ahlstrom learned his taxonomy and systematics from freshwater plankton. In the early forties, he produced revisions of the rotifer genera *Brachionus* and *Keratella* which are still valid today. It was this taxonomic experience that gave him the confidence to step up to larval fish and "to study the larvae of all the abundant fish species rather than sardines alone" (editors).

This volume is a compendium of studies from many workers and laboratories. The first section, Modelling, was introduced by Geoffrey C. Laurence, United States. He believes "the emphasis of future larval research should include studies of population structure and internal functional mechanisms of larval fish predators and fine scale distribution and abundance studies of larval food organisms." He pleads for a multidisciplinary approach as do several other chairmen. The second section, Pollution, was introduced by Åke Granmo, Norway. He concludes that newly hatched larvae are more sensitive to pollutants than embryos and that both embryos and larvae are more sensitive than adults. Heavy metals and other pollutants produce "spinal abnormalities, curved tails, higher frequency of abnormal eye and brain development, increased mortality and impaired hatching." The third section, Enclosure Studies, was introduced by Per Solemdal, Norway. He concludes that enclosure studies are especially useful for studing growth and mortality, effects of pollution, and various aspects of mariculture. Future studies should test and improve our present methodology. The fourth section, Distribution and Abundance, was introduced by A. Saville, Great Britain, and D. Schnack, West Germany. They indicate that "these applied aspects produce the main forces and financial backing necessary for the study of the distribution and abundance of the early life history stages of fish on an adequate scale." They also state that "At the present time, however, studies of distribution and abundance, are being directed in two major directions: a) determining spatial and temporal distributions in the near coastal zone chiefly to provide background information against which the effects of industrial interference with the environment can be evaluated, and b) obtaining some fisheries-independent measure of exploited stocks." The fifth section, Physiological Ecology, was introduced by the editors, R. Lasker, United States, and K. Sherman, United States. They attribute the interest in this field during the last 30 yr to two reasons: "1) the newly found ability to apply information on fish eggs and larvae to fisheries and aquaculture problems and 2) the academic interest in survival of fish species." The sixth section, Rearing and Aquaculture, was introduced by A. Jones, Great Britain. He believes that the inconsistencies in survival and quality of reared fry underlines a need for continued effort to improve problem areas, and that further study is required in four areas: 1) refining techniques for controlling spawning times in captive brood stocks, 2) developing and using artificial food to reduce costs and increase health, 3) investigating specific environmental requirements of important larvae and, 4) improving the design and operation of hatcheries. The seventh and last section, Systematics and Development, was introduced by E. H. Ahlstrom, United States, and H. G. Moser, United States, with an excellent paper entitled "Systematics and development of early life history stages of marine fishes: achievements during the past century, present status and sug-

gestions for the future." They indicate that the eggs and larvae are known for slightly over 200 families out of a worldwide total of 450 families. They provide an impressive list of suggestions for future study including: improvement of collecting, handling, preserving and storage techniques; evaluation of the variability of larval characteristics; and better utilization of larval characteristics to develop systematic relationships.

The overall size of this soft-cover volume (20.5 × 25.5 cm) is intermediate; it is larger than a book but smaller than many other publications having to do with early life history studies. The occurrence of abstracts throughout the volume seems to be haphazard for many small papers and a few long and complicated ones lack them. The endings of papers sometimes leave entire pages empty adding to its cost and thickness. I believe it would be useful to have an author index because of the large numbers of authors who contributed. Because authors were required to bring their completed manuscripts to the conference, a period of $2\frac{1}{2}$ yr is entirely too long from submission to publication. As a result, some papers are only abstracts or short summaries of the presentations given at Woods Hole. Fortunately or unfortunately, entire studies have been published elsewhere. This volume has been carefully edited and contains few errors in typing and formating, thus congratulations to the Dartmouth Staff of the North Atlantic Fisheries Organization (NAFO) (previously ICNAF) for their publication production achievements. At slightly more than a nickel a page, this volume is a bargain at today's prices.

I highly recommend this book because it is a compendium of significant early life fishery papers and because I believe many of the scientific leaders in the early life history of fishes within the next few decades are among the authors. There is abundant information in this publication for students, biologists, fishery managers, and even administrators, but one has to read several papers to get a message. These papers suggest that early life history studies can be useful to research and elucidate fundamental problems in pollution, population dynamics, aquaculture, physiology, etc. It is hoped this volume will stimulate further support from both the scientific community and administrators in this area of fisheries.

SMITH, P. E., AND S. L. RICHARDSON. 1979. Selected bibliography on pelagic fish eggs and larva surveys. FAO Fish. Circ. 706: 97 p.

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(R430)

Stress and Fish. *Edited by A. D. Pickering, Academic Press Inc. (London) Ltd., England. 1981. 367 p. $59.50. £24.60.*

The book is based on 14 invited papers given by internationally recognized experts at the Fisheries Society of the British Isles International Symposium, "Stress in Fish," held at the University of East Anglia, Norwich, England, September 9–12, 1980. Abstracts of both oral and poster papers are included. A fish species index is found at the end of the book but there is no author index. The subject index is adequate but not overly detailed, and there is an unevenness that may be associated with this kind of volume.

The title, *Stress and Fish*, is somewhat illusory. In the introductory chapter, The Concept of Biological Stress, the editor states that "stress will be used to describe a stimulus, the reaction of the system the stress response." If so, virtually every significant interaction a fish has with its environment, is, by definition, a stress. The numerous physical and chemical stimuli perceived by fishes may be classified wrongly as stressors even though they fall within a normal pattern. The word stress might be better used to define noxious stimuli or those which fall outside of the normal range and lead to a deleterious and/or abnormal physiological response. The difference between the two terms stimulus and stress, in this context, is not clear to the reviewer. Perhaps the title could have been, for example, physical and chemical factors in relation to the environmental physiology of fishes.

Chapter 2 by Edward M. Donaldson outlines researches, largely his own, on the response of the pituitary–interrenal axis as an indicator of stress in fishes. As in mammals, the adrenocortical cells are responsive to the increased secretion of ACTH from the pituitary gland. However, in fish, as in the higher vertebrates, endocrinologists have been less successful in defining the nature of the secondary response to adrenocortical steroids in terms of their protective action against stress. These secondary actions are relatively clearer in relation to adrenergic responses to stress in fish. M. M. and F. Mazeaud define some of the physiological changes that occur in response to catecholamine release from cells which are homologous with those of the mammalian adrenal medulla.

F. B. Eddy gives a general account of some of the principles of osmotic and ionic regulation in fish, followed by an examination of the changes following the impact of osmotic stress, temperature changes, environmental acidification, and inorganic pollutants. The critical effects of handling and anesthetics on osmotic and ionic regulation point to the need to minimize this kind of stress to improve experimental design. Section III of this chapter, entitled "Endocrinology of Osmotic and Ionic Regulation" is, in my opinion, thin, probably due to the limitation of space.

The effects of inadequate oxygen and pollutants on the respiratory system in bony fishes are considered by G. M. Hughes, in relation to the importance of neural and neuroendocrine functions in the total response of fishes to environmental stimuli. The author states that respiratory physiologists should probably not use the term stress when there is inadequate evidence that either catecholamines or adrenocortical steroids are involved in regulatory processes; a very narrow definition of stress compared with that given by some contributors, particularly A. D. Pickering in the introductory chapter.

A. E. Ellis explains how defence mechanisms are modulated in fishes in response to stress. It shows how stress and resistance to disease are related, often through complex interactions, albeit there is virtually no information about fishes. Lymphocyte function is considered in relation to stress and the hormonal factors associated with it.

Chapter 10 entitled Some Aspects of Thermal Stress on Freshwater Teleosts by J. M. Elliot is particularly useful. The author defines thermal stress in fish as "any temperature

change that produces a significant disturbance in the normal functions of a freshwater teleost and thus decreases the possibility of survival." In this excellent chapter such responses to thermal stress as tolerance, resistance, and metabolic adjustments are considered. The chapter is based largely on the pioneering work of Prof F. E. J. Fry.

The chapter entitled Methods for Determining the Tolerance of Fishes to Environmental Stressors seems to be unsubstantial at times. For example, in Table I, entitled "A Summary Interpretation of Physiological Tests to Assess the Effects of Environmental Stressors on Fish," the material seems to be too general and vague to be of use as a significant diagnostic tool.

Other chapters are interesting and valuable, particularly Chapter 13, Stress and Compensation in Teleost Fishes: Response to Social and Physical Factors.

In summary, this is a very worthwhile book containing an excellent account of aspects of the physiology of stress and the impact of environmental factors on fish physiology. This book will be extremely useful for field biologists, fisheries scientists, and academics. I warmly recommend it.

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(R412)

Books Received / Livres reçus

November / novembre 1982

Fishes of the Western North Atlantic: Part 8, Order Gasterosteiformes, Suborder Syngnathoidei. Sears Foundation for Marine Research Memoir Number 1. *C. E. Dawson and Richard P. Vari. Sears Foundation for Marine Research, Yale University, New Haven, Connecticut. 1982. xi + 198 p.* This volume includes accounts of 32 species in 11 genera and 3 subfamilies of pipefishes and seahorse, all commonly encountered by inshore fishermen. Each account combines a review of published knowledge. (R461)

Mathematical Models in Biological Oceanography. *Edited by T. Platt, K. H. Mann, and R. E. Ulanowicz. Monographs on oceanographic methodology 7. The Unesco Press (United Nations Educational, Scientific and Cultural Organization), Paris. 1981. 156 p.* This volume represents the first fruits of the labors of the SCOR (Scientific Committee on Oceanic Research) Working Group 59 set up in 1977. The terms of reference included the following: (1) to suggest mathematical methods in marine ecology for the design of research programs in the open sea and the nearshore waters, and (2) to suggest experiments for the treatment of biological data collections with particular reference to the development of mathematical models. (R462)

Encyclopedia of Marine Invertebrates. *Edited by Jerry G. Walls. T. F. H. Publications Inc., Ltd., Neptune, New Jersey. 1982. 736 p. (hard cover, 5½ × 8″). $49.95 (U.S.).* Included are 619 color photos, 38 black and white photos, and 187 line drawings. Emphasis is placed on groups that are kept in marine aquaria with specific information on their habits, life history, and ecology. The book was designed to serve the average informed reader and stands as a background for the technical literature. (R463)

Histology of the Striped Bass. *David G. Groman, American Fisheries Society Monograph Number 3. American Fisheries Society, Bethesda, Maryland. 1982. vi + 116 p. $12 (U.S.) in the United States, $13.80 (U.S.) elsewhere.* This atlas was developed to provide a reference for those concerned with the health maintenance of striped bass propagated under intensive aquaculture conditions. Because it includes discussions and photographs of all major organ systems from normal fish, it should be useful to those who need to assess abnormal or pathologic changes in field and laboratory specimens. (R464)

Ecological Stress and the New York Bight: science and management. *Edited by Garry F. Mayer. Estuarine Research Federation, Columbia, South Carolina. 1982. ix + 715 p. paperback, $10 (U.S.).* Proceedings of a symposium held in 1979 and organized and funded by the NOAA's (National Oceanic and Atmosphere Administration's) MESA (Marine EcoSystem Analysis) New York Bight Project. Its purpose was to summarize evidence on the effects of human wastes on the biota and ecosystems and to assess possibilities for improving the management of major sources of marine pollution in the region. Included are detailed technical reports on specific research efforts and panel reports aimed at a wider readership. (R465)

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Announcements/Avis **J. Watson**

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Adaptive flexibility in the foraging behavior of fishes **L. M. Dill**

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Analysis of the biological and demographic parameters of northern sand lance, *Ammodytes dubius*, from the Newfoundland Grand Bank **G. H. Winters**

Normal ranges for diagnostically important hematological and blood chemistry characteristics of rainbow trout (*Salmo gairdneri*) **W. R. Miller III, A. C. Hendricks, and J. Cairns Jr.**

Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980 **N. J. Bax**

Sea urchins in the Saint Lawrence Estuary: their abundance, size-structure, and suitability for commercial exploitation **J. H. Himmelman, Y. Lavergne, F. Axelsen, A. Cardinal, and E. Bourget**

Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival **P. J. Tschaplinski and G. F. Hartman**

Evidence of acidification of some Nova Scotian rivers and its impact on Atlantic salmon, *Salmo salar* **W. D. Watt, C. D. Scott, and W. J. White**

An echo counting and logging system (ECOLOG) for demersal fish size distributions and densities **L. M. Dickie, R. G. Dowd, and P. R. Boudreau**

Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie **J. M. McCuaig and R. H. Green**

Genetic differentiation in the face of gene flow: a study of mussel populations from a single Nova Scotian embayment **K. E. Gartner-Kepkay, E. Zouros, L. M. Dickie, and K. R. Freeman**

Early growth and quality of chum salmon (*Oncorhynchus keta*) produced in keeper channels and gravel incubators **R. A. Bams**

A test of lead-210 dating for the measurement of whole lake soft sediment accumulation **R. D. Evans and F. H. Rigler**

An investigation of the relationship between Oregon coho salmon (*Oncorhynchus kisutch*) hatchery releases and adult production utilizing law of the minimum regression **J. Clark and B. McCarl**

Management analysis of the Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model **G. L. Swartzman, W. M. Getz, R. C. Francis, R. T. Haar, and K. Rose**

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Frederick Ronald Hayes, 1904–1982 **L. M. Dickie**

Francis Derwood McCracken, 1916–1982 **W. B. Scott**

Donovan Bartley Finn, C.M.G., 1900–1982 **H. C. Winsor**

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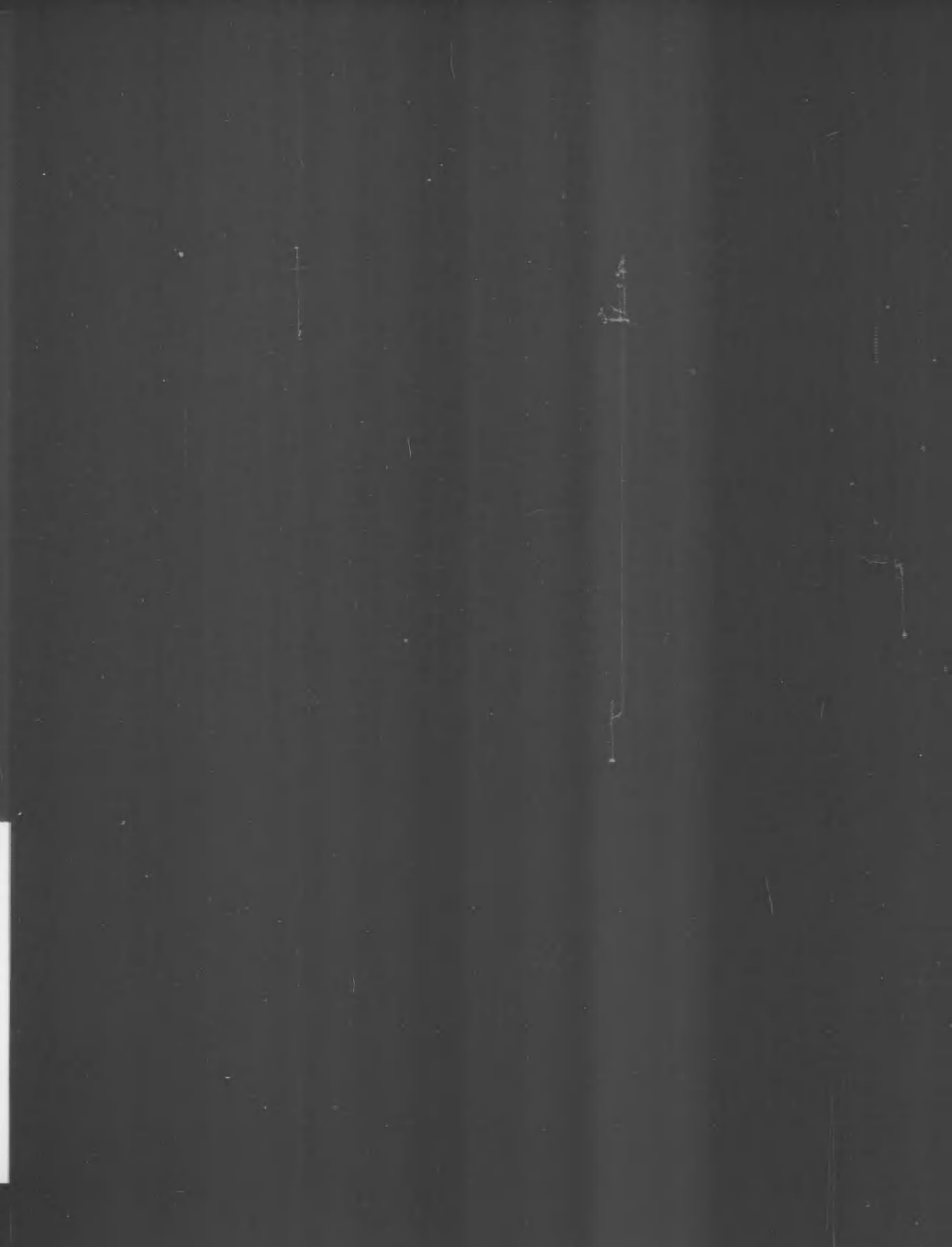
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